

DYNAMICS OF THE NORTHERN FLICKER HYBRID ZONE: A TEST OF THE
BOUNDED-HYBRID SUPERIORITY HYPOTHESIS

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ABSTRACT

The bounded-hybrid superiority hypothesis (BHS) predicts stable hybrid zones are characterized by hybrids having the highest fitness within the zone. The dynamic-equilibrium hypothesis (DEH) predicts hybrids to have the lowest fitness and mating should be strongly assortative in the hybrid zone. I used phenotypic-based hybrid indices (HI) to assess mating patterns, reproductive success, and survival of hybridizing northern flickers (*Colaptes auratus*) within the hybrid zone at Riske Creek, British Columbia.

Contrary to the BHS, flickers showed significant assortative pairing ($P = 0.038$) which may result via passive mate choice if yellow and red flickers migrate from allopatric winter ranges. North American band recoveries show red-shafted and yellow-shafted flickers winter on different sides of the Rocky Mountains while red-orange hybrids from Riske Creek winter in the range of red-shafted flickers. Arrival dates of phenotypes did not support the idea that mating patterns are caused passively via different arrival schedules. However, assortative mating patterns did correlate with regional weather patterns along flicker migration routes as well as the North Atlantic Oscillation (NAO) a continental weather pattern that has been shown to influence various aspects of the annual cycle in other birds. If variable weather patterns result in different mating patterns by affecting migration, the geographic location of the northern portion of the zone may be variable due to the migratory behaviour of individuals.

There were no differences among yellow, orange and red flickers to win more agonistic contests or have earlier nest initiation dates, larger clutch sizes, greater hatching success, or produce more fledglings. No colour group had a higher likelihood of having a successful compared to a depredated nesting attempt. Aggression was

similar between red ($N = 21$) and yellow flickers ($N = 20$) during taxidermy model presentations of pure red-shafted and yellow-shafted flickers. Using Akaike's information criterion (AIC) in Program MARK, I determined survival was best modeled as either constant between males and females or varying annually according to weather. Models incorporating HI had less support but suggested that survival is best modeled as a linear relationship where red-shafted flickers have the highest survival. Survival modeled in quadratic relationships found hybrid flickers to have the highest apparent survival estimates in support of the BHSH. Overall there was no support for reduced hybrid fitness, but survival appears to be influenced more by annual variation rather than strictly by an individual's HI. Overall, I failed to find reduced hybrid fitness in support of the DEH but also failed to find increased hybrid fitness as predicted by the BHSH. Annual changes in selection pressure could prevent introgression of hybrid genes throughout the zone if selection favours red-shafted genes in some years and yellow-shafted genes in other years.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

Hybridization is widespread in nature; among birds, almost 10% of all described species have had a documented case of hybridization with another species (Grant and Grant 1992). Hybrid zones are areas where two genetically differentiated populations occur in sympatry and successfully interbreed to produce at least partially fertile offspring (Arnold 1997). Hybrid zones provide “natural laboratories” to study and understand evolutionary forces (Barton and Hewitt 1989; Harrison 1993; Coyne and Orr 2004).

Generally, hybrid zones occur after secondary contact between populations which differentiated in allopatry, but for which reproductive isolating mechanisms have not evolved (Mayr 1963; Hewitt 1988). For example, within North America, recent ice ages likely separated populations for thousands of generations, allowing for divergence as selection favoured those individuals most suited to the local conditions. Upon glacial retreat, the two populations (which may differ in morphology, genetics, behaviour or in other regards) came into contact as the landscape revegetated, allowing hybridization to occur. Alternatively, varying environmental gradients may allow once-separated populations to expand towards each other during times of environmental change (Yang and Selander 1968) or else two species may come into contact with one another after

large-scale changes in habitat or vegetation caused by humans (Gill 1980; Rohwer and Wood 1998).

Historically, hybrid zones were considered ephemeral, leading either to speciation through reproductive isolation (if hybrid offspring were less fit than parental types) or else fusion of the two forms into a single species (if hybrid fitness was equal to parental types; Dobzhansky 1940). In the first case, a narrow hybrid zone may persist if reproductive isolating mechanisms have not evolved and the hybrids are trapped by steep selection gradients (Szymura and Barton 1986). Alternatively, the hybrid zone may persist if hybrids are more fit than parental types within the hybrid zone but less fit outside the zone of contact (Moore 1977). Traditionally, most zoologists have seen hybridization as a failure of reproductive isolation mechanisms that results in offspring that are inferior to pure parental types (Darwin 1859; Dobzhansky 1935, 1940; Mayr 1963; Barton and Hewitt 1981; Arnold 1997). More recently, theory and empirical data suggest that hybrids can have higher fitness relative to pure parental types within a hybrid zone (Endler 1973; Moore 1977; Arnold and Hodges 1995). For example, Good et al. (2000) found pairs containing hybrid males produced larger clutches and fledged more chicks compared to pairs containing pure western gull (*Larus occidentalis*) males and had better fledging success than pairs involving pure glaucous-winged gulls (*L. glaucescens*) males.

1.2 Distinguishing Types of Hybrid Zones

Clearly, multiple factors or conditions underlie hybrid zones and different dynamics will be responsible for different types of hybrid zones. Moore and Buchanan (1985) suggested the northern flicker hybrid zone was stable by comparing the phenotype of collected specimens over several decades. Even though these specimens had very

similar distributions, a lack of evidence showing zone expansion through dispersal of yearlings or contraction of the zone through reduced hybrid fitness (Moore and Koenig 1986) further suggests that the hybrid zone is stationary (although see McGillivray and Biermann 1987). Assuming the flicker zone is stable, there are two major hypotheses to explain the persistence of the zone. These can be distinguished by measuring the relative fitness of hybrids compared to parental types, and by assessing the strength of assortative mating (Table 1.1).

The dynamic-equilibrium hypothesis (DEH) allows for the possibility that narrow hybrid zones may be stable and persist although hybrids have lower fitness than parental types (Barton and Hewitt 1985, 1989). Narrow zones of overlap are where hybrids are confined to small areas by steep selection gradients and reproductive isolation between parental populations is not completely effective (Moore 1977). These steep selection gradients are maintained by a balance between selection against hybrids and dispersal of individuals into the zone resulting in hybrid zones that are much narrower than corresponding environmental gradients (Barton & Hewitt 1985; Barton and Gale 1993). Because hybrids are less fit, there should be selection for increased assortative mating resulting in a reduction of hybrid offspring. However, in the long term, the hybrid zone is maintained by naïve parental individuals immigrating to the zone of contact and not mating assortatively due to reduced availability of their own phenotypes (Hewitt 1988). The main prediction of this hypothesis is that hybrids have lower reproductive success and survival than parental types. One would also expect some (but not complete) positive assortative mating (Table 1.1). According to this hypothesis, the location of the hybrid zone on the landscape is independent of underlying environmental gradients.

Table 1.1 Predictions of the hypotheses for hybrid zones. Dashed lines indicate no specific prediction.

	Ephemeral-zone hypothesis	Dynamic-equilibrium hypothesis (DEH)	Bounded-hybrid superiority hypothesis (BHSH)	Selection-hybridization hypothesis
Hybrid zone stability	Eventually disappears	Stable	Stable	Stable
Fitness of hybrids and parentals	Fusion: hybrids highest Speciation: hybrids lowest	Hybrids less fit than parentals	Hybrids more fit than parents in hybrid zone only	Variable (annually dependent)
Assortative mating	----	Selection for	Selection against in hybrid zone	----

The bounded-hybrid superiority hypothesis (BHSB) predicts in the geographic core ranges of the parental populations, selection favours the parental phenotypes such that few hybrids persist in those areas. However, in the hybrid zone, selection favours hybrids because they have higher fitness there than either of the parental types (Moore 1977; Millar 1983; Good et al. 2000). Fitness of the phenotypes varies according to environmental gradients and therefore according to geographic location, making predictions of assortative mating complex. Within the core geographic ranges of the parental types, there should be selection for assortative pairing but within the hybrid zone, there may be selection for disassortative pairing (if hybrid offspring have the highest fitness there) or preference for hybrid mates if those individuals are most fit within the hybrid zone. In general, one would not expect selection for positive assortative pairing in the hybrid zone according to the BHSB (Table 1.1).

The selection-hybridization hypothesis can be considered a subset of the BHSB except that the underlying environmental gradients vary over time (e.g. annually varying weather influences food availability). As a result, hybrids are superior to parental types in some, but not all, years (Grant and Grant 1992, 1993; Bell 1997). Thus, a balance is maintained where numbers of hybrids in the population fluctuates over time, but the hybrid zone is maintained in the long term. This hypothesis does not make specific predictions about assortative mating. Annual variation in reproductive success and survival that selected both for and against hybrids over time would support the selection-hybridization hypothesis (Table 1.1).

1.3 Study Species

The northern flicker (*Colaptes auratus*, hereafter flicker) is the most common woodpecker in North America, occupying diverse habitats from Mexico to the treeline in

the Arctic (Moore 1995). Although flickers are primary excavators and produce the majority of the nesting cavities at Riske Creek (Martin and Eadie 1999), they readily reuse cavities (Aitken et al. 2002; Wiebe et al. 2007). About 21% of nests fail annually because of predators such as red squirrels (*Tamiasciurus hudsonicus*) and competitors, namely European starlings (*Sturnus vulgaris*) (Wiebe 2003; Fisher and Wiebe 2006b). Flickers lay relatively large clutches, up to 12 eggs (Wiebe et al. 2006), and males invest greatly in parental care, doing more of the cavity excavation, incubation and brooding than females (Wiebe 2005). Annual survival is estimated at 43% for both males and females, and shows no difference with age (Fisher and Wiebe 2006a). While southern populations are largely resident, most flickers in Canada seem to migrate to the United States for winter (Moore 1995; Brewer et al. 2000).

The northern flicker is comprised of five subspecies that are phenotypically distinct (AOU 1983). The western red-shafted flicker (*C. a. cafer*) and eastern yellow-shafted flicker (*C. a. auratus*) hybridize from Alaska to Texas in one of the best documented avian hybrid zones in North America (Short 1965; Moore and Price 1993). Flickers in the hybrid zone show variable intermediate phenotypic traits between those of red-shafted flickers and yellow-shafted flickers. Several studies of the flicker hybrid zone have been conducted in the central and southern United States (Short 1965; Bock 1971; Anderson 1971; Rising 1983; Moore and Buchanan 1985; Moore and Koenig 1986; Moore 1987; Grudzien et al. 1987; Moore et al. 1991) but the northern portions of the hybrid zone are less studied (Rising 1983).

Research on the southern part of the hybrid zone suggested it was stable (Moore and Buchanan 1985) and pairing was random with respect to phenotype (Moore 1987). Although data on clutch sizes indicated that hybrids did not perform significantly better

than parental types in the hybrid zone, at least they did no worse and so the BSHH was accepted (Moore and Koenig 1986). In contrast to these results, McGillivray and Biermann (1987) suggested the northern part of the hybrid zone was not stable and Wiebe (2000) found assortative mating in a northern population comprised of migratory flickers using one year of data. Wiebe and Bortolotti (2001) hypothesized that migration could be influencing hybrid zone dynamics in the north yet the effect of migration has rarely been explored for any hybridizing species (Perez-Tris et al. 2003). Thus, despite flickers often being cited as an example of the BSHH, those claims are based on fairly small sample sizes and some results that conflict with the predictions of this hypothesis. As well, the dynamics of the hybrid zone may be much different in the north.

My objective is to test the predictions of the BSHH and alternative hypotheses for stable hybrid zones (Table 1.1). In chapter 2, I test for patterns of assortative mating using a nine-year data set and investigate the role of migration on these pairing associations. In chapters 3 and 4, I test the prediction that hybrid flickers should have higher fitness than parental types. As surrogates of fitness I consider reproductive performance at several breeding stages including territory defence, laying date, clutch size, hatching success and fledging success in chapter 3. Finally, in chapter 4 I examine survival and recruitment rates according to phenotype.

1.4 General Methods

1.4.1 Study area

The study area was located near Riske Creek, central British Columbia (51°52'N, 122°21'W) and encompassed approximately 100km² of grasslands with scattered trembling aspen (*Populus tremuloides*) and patches of mixed forests of Douglas fir (*Pseudotsuga menziesii*), hybrid spruce (*Picea engelmannii* x *P. glauca*) and lodgepole

pine (*Pinus contorta*; Martin and Eadie 1999; Wiebe 2000). Here there is a range of phenotypes in the flicker population with most displaying hybrid characteristics (Erskine 1962; Wiebe 2000). Flickers begin to arrive on site after migration in the latter half of April with territory establishment and nest excavation occurring soon thereafter.

1.4.2 *Monitoring nests and capturing adults*

Between 1998 and 2006 approximately 80-140 nest sites were monitored annually. Nests were discovered by broadcasting flicker calls in early spring by soliciting responses from territorial flickers to locate active territories and by checking all old sites from previous years. I used vocalizations recorded in California from A Field Guide to Western Bird Songs: Western North America (Peterson Field Guide Audio Series, Cornell Lab of Ornithology, Houghton Mifflin, Boston, Massachusetts). There are no known differences in the vocalizations between yellow-shafted and red-shafted flickers (Moore 1995) so my ability to detect the subspecies should not have been biased. Once a territorial pair responded, cavities in the surrounding tree clumps were checked every few days to determine the onset of egg laying. During this time I noted if the male and female were already colour-banded or new to the study. Once an active nest was found, it was monitored by cutting a small, replaceable door into the tree trunk to allow access to the eggs and nestlings (Wiebe 2000, 2002). Subsequently, nests were visited approximately every four days with a ladder, flashlight and mirror to determine clutch size, nest fate and hatching date.

Flickers were captured on nest by flushing birds into a net placed over the entrance hole either as they incubated eggs or brooded chicks, or flew into the cavity to provision young. After capture, adults were banded, sexed, aged, weighed, and scored on various plumage attributes (see, chapter 1.4.3 Calculating a Hybrid Index). Flickers can easily

be sexed by plumage because females lack the malar (mustache) stripe while accurate aging to four years in woodpeckers, including flickers, is done based on moult patterns (Pyle 1997). In analyses involving age, I pooled adults into three categories: 1 year old (first breeding attempt), 2 years old (second breeding attempt), and 3+ years (at least third breeding attempt). Adults were banded with a U.S. Fish and Wildlife Service aluminum band and a unique series of colour bands to allow individual recognition in the field. Previously banded birds were not targeted for recapture in subsequent years although they were sometimes retrapped circumstantially when the identity of the individual in the cavity was unknown. Both adults were banded at > 95% of nests each summer.

1.4.3 *Calculating a hybrid index*

Studies of hybridization assume genotypic differences between the two populations; however, research aimed at quantifying the underlying genetic make-up of flickers is currently not available. Recent publications on hybridization still largely rely on phenotypic hybrid indices (HI), assuming that such indices meaningfully reflect genotypes at least in ordinal rankings (W.S. Moore, pers. comm.). A recent study confirmed that underlying genetic differences in hybrid sharp-tailed sparrows (*Ammodramus nelsoni* and *A. caudacutus*) was correlated with a plumage variation index (Shriver et al. 2005), suggesting that phenotypic HI are meaningful to test hypotheses of hybridization. Thus I calculated HI for flickers to compare assortative mating, reproductive success, and survival between different phenotypes.

Calculating a HI involves some subjectivity and so I calculated several types of HI and compared their performance in analyses to see if my conclusions were robust over a range of different methods. Two HI were based on categorical plumage rank scores.

Following Short (1965), I scored throat, ear, nuchal, shaft (mean of tail rachis and vane) and mustache (males only) on a 5-point scale where 0 = pure *auratus* and 4 = pure *cafer* (Table 1.2), omitting crown scores because Moore (1987) suggested those were unreliable. However, the boundaries of Short's (1965) categories were arbitrary, for example, mustache categories (as % black) were set as 0%, 1-20%, 21-79%, 80-99%, and 100%, lumping a large range of hybrids into a single intermediate category between 21-79%. Therefore, in addition to Short's system, I categorized traits (throat, ear, and mustache) in a second way using more even divisions of 0%, 1-33%, 34-66%, 67-99% and 100% that I called 'Riske Index'. These two HI gave slightly different P-values in correlations of assortative mating but the direction of trends was always consistent. I chose to present results using the 'Riske' scoring scheme which divided the individuals more evenly among categories but my general conclusions would not differ from those using the Short scoring method.

Since traits vary on a continuum between pure forms it would be ideal to score each on a continuous scale rather than categorical scores. However, only tail feathers provided a large enough area of consistent colour that I could sample in the field and quantify objectively using a spectrophotometer. Tail feathers were not collected from all individuals, but for flickers in 1998-2000 and 2005-2006, I used a spectrophotometer (Konica Minolta Sensing, Inc., model CM-2600d) for a measure of rectrix colour. There are several methods to quantify spectral reflectance to allow comparisons between colour groups of interest (Endler 1990). While Principal Component Analysis (PCA) is best used when quantifying complex colour patterns, it also provides an unbiased method to compare simple spectra as found in tail colour of flickers (e.g. Uy and Stein 2007). I used PCA analysis because it provided a continuous measure of individual

hybridness that satisfied the assumptions of statistical tests (e.g. ANOVA) that I used to compare several variables of interest between flickers of different phenotypes.

The spectrophotometer measured light between 360nm-740nm but preliminary data analysis showed that most variation in colour differences among flicker feathers was explained by wavelengths between 570nm and 700nm. Therefore, I considered spectral reflectance values between 570nm-700nm (the portion of the spectral range encompassing yellow, orange, and red) to enter into a PCA analysis (Cuthill et al. 1999) and extracted on two axes. The score on the first axis (PCA1) differentiated brightness values that are usually independent of colour (Cuthill et al. 1999). For all feathers the score on the second axis (PCA2) had a mean value of 0 and a standard deviation of 1 where negative PCA2 values corresponded with red feathers and positive PCA2 values correspond with yellow feathers. The PCA2 value differentiated between red, orange and yellow feathers and was consistent with my categorical scores used in the field (Fig. 1.1). Setting the PCA score of the most yellow feather to a "zero" baseline, I divided each feather's score by the score of the reddest feather to obtain a continuous ranking from 0 (most yellow) to 1 (most red). I standardized feather scores in this manner so that all HI varied between 0 and 1 to allow for comparisons of relationships of mating patterns, reproductive success and survival between the different HI. These scores were incorporated into some hybrid indices (see below).

Since not all plumage traits were recorded for each individual in each year, I standardized the sum of the categorical plumage traits on a scale of 0 (pure *auratus*) to 1 (pure *cafer*). I then calculated three hybrid indices: HI1 used only the scored (Riske categorical) plumage traits, HI2 used scored plumage traits but substituted the

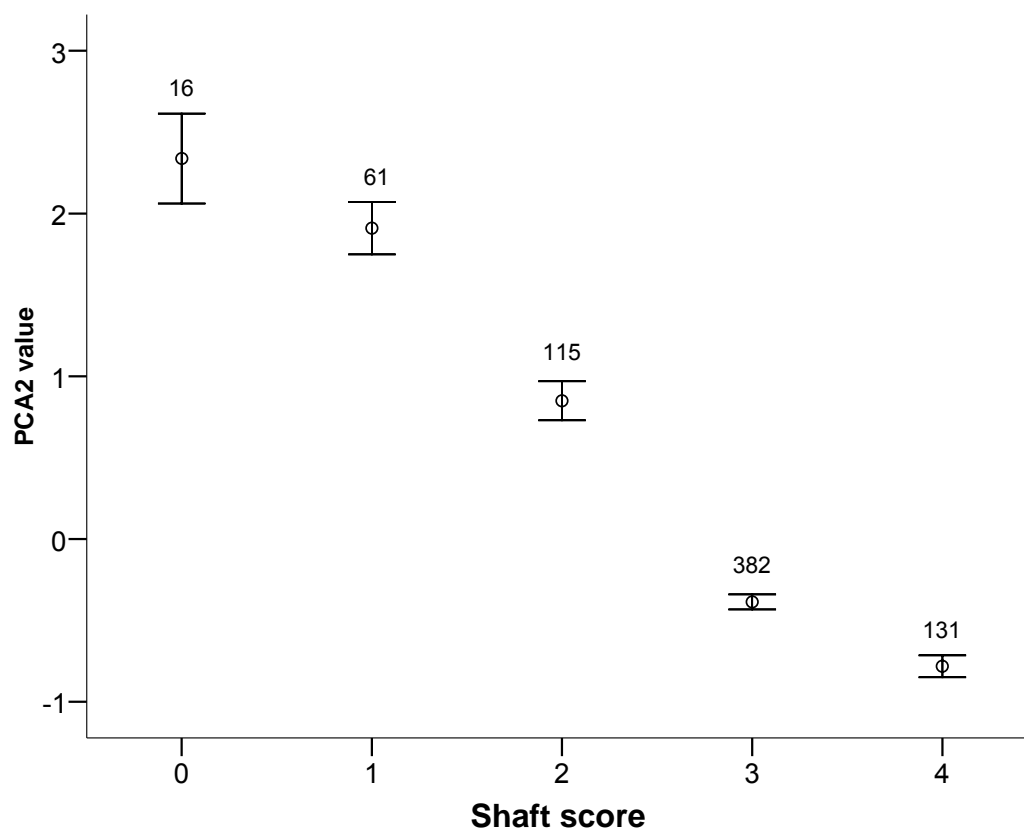


Figure 1.1 Mean and 95% CI of the categorical score assigned in the field and PCA2 values from the spectrophotometer. Shaft scores of 0 are yellow feathers as in *auratus* and shaft scores of 4 are red as in *cafer* following Table 1.2. Negative PCA2 values are red feathers and positive PCA2 values are yellow feathers. Samples sizes are provided above each error bar.

continuous tail colour for the categorical tail colour score, and HI3 which was the continuous rectrix score from the spectrophotometer.

Sample sizes for HI2 and HI3 were smaller than HI1 because tail feathers were not collected from all flickers in all years.

Scoring of HI1 was quite consistent as suggested by the fact that of seven birds trapped and phenotypically scored twice in the same season by Karen Wiebe, no plumage traits were ranked differently except for 1 case of tail colour shifting by 1 category (paired t-test: $t = -0.24$, $df = 7$, $P = 0.81$). Individuals trapped and scored in different years also maintained the same phenotype (paired t-test: $t = -0.06$, $df = 182$, $P = 0.96$). Based on this, in cases when a previously colour-banded bird was not recaptured in a given year, I used its HI from last capture. Wiebe and Bortolotti (2002) documented a slight shift to more reddish tail feathers with age detectable only with a digital camera and not by eye. Spectrophotometer results on a larger sample of feathers showed a similar, but non-significant trend (paired t-test $t = -1.57$, $df = 68$, $P = 0.12$).

Table 1.2 Scores and descriptions of colour characters used to score flickers captured at Riske Creek, British Columbia, between pure yellow-shafted (*auratus*) and pure red-shafted (*cafer*) forms. Modified from Short (1965).

Character and Score	Description
Ear coverts	
0	Vinaceous tan, as in <i>auratus</i>
1	Gray traces (67-99% tan)
2	Intermediate (34-66% tan)
3	Tan traces, especially below eye (1-33% tan)
4	Gray, as in <i>cafer</i>
Throat colour	
0	Vinaceous tan, as in <i>auratus</i>
1	Gray traces, usually on lower throat (67-99% tan)
2	Mixed gray and tan (34-66% tan)
3	Tan traces, usually near chin (1-33% tan)
4	Gray, as in <i>cafer</i>
Nuchal patch	
0	Present, broad, as in <i>auratus</i>
1	Present, restricted in width
2	Present, broken in one or more places
3	Traces, usually at sides of nape
4	Absent, as in <i>cafer</i>
Shaft colour	
0	Yellow, as in <i>auratus</i>
1	Orange traces, usually faint in all feathers
2	Shafts orange or red, barbs yellow-orange
3	Orange-yellow
4	Salmon pink, as in <i>cafer</i>
Malar colour (males only)	
0	Black, as in <i>auratus</i>
1	Some red (1-33% red)
2	Intermediate (34-66% red)
3	Some black (67-99% red)
4	Red, as in <i>cafer</i>

CHAPTER 2

ASSORTATIVE MATING WITHIN THE NORTHERN FLICKER HYBRID ZONE AND THE ROLE OF MIGRATION

2.1 Introduction

Assortative mating, the pairing of individuals with similar phenotypic traits in a non-random pattern (Burley 1983), is of interest to evolutionary biologists because it is one way to reinforce premating reproductive isolation between phenotypes in hybrid zones (Dobzhansky 1937; Mayr 1942; Coyne and Orr 2004). Assortative mating may arise through active mate choice where individuals seek mates that are similar to themselves (like preference), or where a preferred phenotype outcompetes others for a mate of the same preferred type and consequently lower quality individuals pair by default (type preference; Burley 1983). Alternatively, assortative mating may arise by passive choice if types are spatially segregated by habitat preference (Craig et al. 1993; Ferrer and Penteriani 2003) or if phenotype availability is temporally staggered, for example, as a result of migration patterns where phenotypes pair at different times such as in European blackcaps (*Sylvia atricapilla*; Bearhop et al. 2005). Assuming individuals can recognize population divergence when choosing mates, natural selection should favour active “like preference” mate choice if hybrids are less fit than pure parental types (Barton and Hewitt 1985; Liou and Price 1994).

Eastern yellow-shafted flickers (*Colaptes auratus auratus*) and western red-shafted flickers (*C.a. cafer*) hybridize throughout North America from Texas to Alaska. The

hybrid zone has been known since the 1800s yet some dynamics of the zone are poorly known. Moore and Buchanan (1985) suggested the zone was best explained by the bounded-hybrid superiority hypothesis (BHS) which predicts hybrids are most fit within the stable hybrid zone. In support of this hypothesis, there appeared to be no assortative pairing of the subspecies in southern portions of the hybrid zone (Short 1965; Bock 1971; Moore 1987) and no reproductive costs to mixed pairs (Moore and Koenig 1986). However, Wiebe (2000) found assortative pairing in the northern part of the zone where flickers were migratory, and Wiebe and Bortolotti (2001) documented a bimodal distribution of phenotypes and suggested that different arrival and pairing chronologies between yellow-shafted and red-shafted flickers may be partially responsible.

When two populations show different migration strategies to a single sympatric breeding range it is known as a migratory divide (Bensch et al. 1999; Bearhop et al. 2005). Differences in arrival times may impose passive constraints on mate choice due to phenotype availability when migratory divides occur within hybrid zones. Different populations may arrive on the breeding grounds at different times because they winter at different locations and migrate along different routes or at different speeds. For example, blackcaps breed in central Europe and winter in two locations: the British Isles and Iberia (Berthold et al. 1992). Birds that winter in northern areas (Britain and Ireland) react differently to changing photoperiods in spring and arrive at breeding grounds earlier relative to southern populations (Berthold et al. 1992; Bearhop et al. 2005). This leads to assortative pairing between the genetically distinct populations and results in increased reproductive success to early migrants (Bearhop et al. 2005).

Unfortunately, the migration patterns of northern flickers are not well known. There is a paucity of band-recoveries to delineate migratory connectivity and stable isotopes,

which have been used to identify migration routes in other bird species (e.g. Mazerolle et al. 2005b), may be unable to differentiate flicker populations because of overlapping isotope values east and west of the Rocky Mountains (Hobson 2005b; appendix A). Christmas Bird Count surveys suggest yellow-shafted flickers winter east of the Rocky Mountains and red-shafted in the west (National Audubon Society 2002). The distribution of hybrids in winter and the exact migration routes that the different populations follow in spring are unknown. Nevertheless, local and large-scale climatic systems have been shown to influence migration speed, migration routes or arrival patterns in other birds (Ahola et al. 2004; Marra et al. 2005). Large-scale weather patterns such as the El Niño/Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) can affect both timing of breeding (Przybylo et al. 2000; Wilson and Arcese 2003) and migration (Hüppop and Hüppop 2003; Vahatalo et al. 2004; Stervander et al. 2005; Gunnarsson et al. 2006).

If the subspecies of flickers within the hybrid zone winter in different locations or have different migration routes, large-scale weather patterns during migration that vary annually could influence hybrid zone dynamics. If weather patterns affect the movements of the phenotypes differently it could lead to annual variation in the timing and proportion of phenotypes on the breeding grounds. In turn, this could influence annual variation in the prevalence of assortative mating. If weather influences the arrival times of the phenotypes differently, I predicted a correlation between regional or continental weather patterns and the proportions of phenotypes in the population.

In this chapter, my objectives were 1) to test for patterns of assortative mating using a nine-year data set, 2) to review information on migration routes based on band recoveries, 3) to determine whether the arrival times and breeding phenology of the

phenotypes differed in the hybrid zone and 4) to examine the influence of weather on patterns of pairing.

2.2 Methods

Nests were located and breeding adults were captured using the protocols outlined in chapter 1. I only used the first year of the union if mated flicker pairs remained together over successive seasons to avoid pseudoreplication in the correlations. However, when one member of a pair obtained a new mate the following year I considered it a new pairing and included this occurrence. I also excluded pairs that formed after their first nest failed since the pool of available mates may be very restricted late in the season and probably would not reflect arrival of phenotypes in spring.

2.2.1 Assortative mating measurements

The hybrid index in flickers is based on plumage traits that seem to assort independently (Moore 1987) and therefore individuals may show different combinations of "yellow-shafted" and "red-shafted" plumage traits. Since it is unknown whether mate choice could be strongly based on one particular trait as opposed an overall degree of "hybridness" reflected in a composite index, I calculated correlations between all combinations of plumage attributes and between three different HI. I used non-parametric Spearman correlations for the ranked scores of the plumage traits and HI, except for HI3 which was a continuous measure and could be analyzed with Pearson correlations. Correlations were done for all years pooled and also for individual years to determine annual variability in the prevalence of assortative mating. I used the computer program G*Power 3 for some post-hoc power analyses where a non-significant statistical result suggested that my ability to detect and reject a false null hypothesis was limited (Faul et al. 2007).

2.2.2 Linking wintering and breeding locations of flickers in North America

I obtained band-recovery records from the Canadian Bird Banding Office in Ottawa and sightings from individuals originally marked at Riske Creek between 1998 and 2006. I plotted movements of flickers throughout Canada and the United States west of longitude 90°W on a continental scale. I only included records of individuals that were recorded both on a breeding area (April 20 to July 15) and a wintering area (November 15 to February 15). I excluded any distances less than 200km which may represent localized dispersal rather than migration. I broadened the definition of winter to include 1 October to 28 February for hybrids recoveries because the sample was low for the population at Riske Creek. Distance from the study area was not dependent on date of recovery in this sample ($F_{1,13} = 0.06$, $P = 0.80$), suggesting that these individuals were at or near their wintering grounds when the bands were reported.

2.2.3 Arrival of phenotypes to Riske Creek

I monitored arrival dates of yellow and red flickers to Riske Creek in 2006 using taped playbacks of flicker territorial calls. It took 3-4 days to complete one sweep of the entire study area and I made several "rounds" between April 17 and April 30 as detections of new individuals dropped considerably after that date. Flickers here nest in discrete clumps of trees separated by open grassland. Repeated censusing of previously-banded adults in spring showed that they did not change their defended tree clump once they occupied it. However, because most of the birds arriving to breed are unbanded because annual apparent survival is estimated at 43% (Fisher and Wiebe 2006a) there are two considerations that must be made. First, to avoid double-counting the arrival times of unbanded individuals, I only recorded the first sighting of a territorial individual in a certain tree clump and assumed it was the same individual thereafter if its phenotype

was the same. Second, when a flicker was observed, I recorded its general colour class as red, orange, or yellow assessing several plumage traits such as tail colour, nape patch, and mustache colour. While assessing flickers in this manner is not as precise as the HI, I could distinguish between phenotypic extremes (i.e. yellow versus red). I used observations of flickers per hour because sampling effort varied on different days, and conducted a two-sample Kolmogorov-Smirnov test (Siegel and Castellan 1988) to see if the distribution of red and yellow phenotypes differed over time.

I could not observe arrival dates directly in other years but if arrival correlates with nest initiation date then indirect information on arrival times may be obtained by examining the nest initiation dates between phenotypes. I tested this assumption by correlating the known arrival times of banded birds in 2006 with their date of first egg. There was a significant correlation for both males ($r = 0.45$, $P = 0.011$, $n = 31$) and females ($r = 0.50$, $P = 0.028$, $n = 19$) and the interval between arrival and laying was not associated with the HI1 for either males ($F_{1,30} = 0.15$, $P = 0.70$) or females ($F_{1,18} = 0.20$, $P = 0.66$). Therefore, I also analyzed annual variation in laying dates between the phenotypes with ANOVA as a measure of differences in arrival.

2.2.4 The influence of weather patterns

To understand how spring weather may affect pairing patterns and breeding phenology, I correlated annual regional and continental (ENSO and NAO) weather variables with nest initiation date, the proportion of yellow individuals, and the average phenotype (mean HI1 score) in the population. For "regional" weather effects, I calculated mean March and April temperatures from the Seattle-Tacoma Airport, Washington, a location that seems to be along the migration route of many reddish individuals in my population (see Fig. 2.2). For the continental-scale climate variables I

used the El Niño/Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) indices which are linked to large-scale patterns of temperature and precipitation that can vary annually (Hurrell 1995). These weather phenomena are known to affect population dynamics of terrestrial organisms (Sillett et al. 2000; Mysterud et al. 2003) including migration patterns (Hüppop and Hüppop 2003) and reproduction in birds (Nott et al. 2002).

In eastern North America, strong positive phases of the NAO lead to above-average temperatures while negative phases result in below average temperatures and increased snow cover during winter (Wallace and Gutzler 1981; Hartley 1999). The tropical sea surface temperature fluctuations that are associated with the ENSO have a strong influence on the Pacific-North America (PNA) pattern (Horel and Wallace 1981). The PNA influences circulation patterns such that during El Niño years above-average temperatures occur in western North America and below-average temperatures occur in the south-eastern United States; in other years these temperature anomalies are reversed between locations (Wallace and Gutzler 1981). I examined both oscillation indices because they have centers of action over the continental regions where pure parental forms of flickers overwinter. The exact timing of migration in my population is unknown, but if flickers arrive in April, it is reasonable to expect that conditions about two months prior (February) may be those that influence migration timing. Monthly indices for NAO and PNA are based on data standardized for three-month periods (i.e., February patterns are calculated based on January through March mean monthly standardized anomaly fields; <http://www.cpc.ncep.noaa.gov/>).

2.3 Results

2.3.1 Assortative mating patterns

Among 613 nesting pairs, there were three significant positive, and one significant negative correlation between the individual plumage traits (Table 2.1). Only one of the 20 correlations is expected to be significant by chance alone. When comparing the same trait within a pair, throat colour was the only one that was significant. Positive assortative mating was found for HI1 but not HI2 or HI3, however, post-hoc power analyses suggested a weak ability to reject a false null hypothesis for both HI2 (power = 0.32) and HI3 (power = 0.10). The small r^2 in all cases suggested that assortative mating was not particularly strong (Table 2.2, Fig. 2.1).

2.3.2 Migration patterns of flickers based on band recovery data

Only 32 of over 1000 records provided by the bird banding office fit my criteria and three additional records came from observations of banded flickers away from Riske Creek. Yellow-shafted flickers in the northern and central prairies typically migrate to the southern United States west of the Mississippi River. Red-shafted flickers typically migrate west of the Rocky Mountains (Fig. 2.2). Data are scarce but suggest that pure parental forms have segregated winter ranges. All 15 migratory records of hybrid flickers come from birds banded at Riske Creek ($n = 5424$; Fig. 2.2). There was a negative relation between hybrid index and migration distance in this sample but no correlation ($F_{1,11} = 3.54$, $P = 0.087$; power = 0.46), however all individuals were "red to orange" with a HI between 0.56 and 0.88.

2.3.3 Arrival of phenotypes to Riske Creek

Although more red-shafted than yellow-shafted individuals were observed on the study area, there was no significant difference in the pattern of arrival between the two

Table 2.1 Spearman rank correlations between plumage traits of males and females within mated pairs of flickers at Riske Creek. Data are from 1998-2006 but sample sizes differ because not all traits were measured in all years. Significant correlations at $\alpha = 0.05$ are in bold.

		MALE					
		Throat	Ear	Nuchal	Shaft	Mustache	
FEMALE		r _s	0.164	-0.040	-0.107	0.033	-0.011
	Throat	P	0.002	0.629	0.033	0.507	0.828
		n	360	146	397	395	393
		r _s	0.025	0.002	-0.109	-0.026	-0.018
	Ear	P	0.751	0.980	0.153	0.734	0.817
		n	161	144	173	173	172
		r _s	0.106	0.138	0.025	0.016	0.036
	Nuchal	P	0.036	0.088	0.535	0.703	0.376
		n	391	154	596	596	595
		r _s	0.069	0.253	0.076	0.041	0.058
	Shaft	P	0.178	0.002	0.064	0.317	0.153
		n	388	150	604	605	604

Table 2.2 Individuals in mated pairs of flickers at Riske Creek showed positive assortative mating for HI1 but not the other indices (see text for definitions). HI3 was tested with Pearson correlations, the other indices with Spearman rank correlations.

	HI1	HI2	HI3
r_s/r	0.084	0.091	0.038
P	0.038	0.132	0.527
n	613	274	274

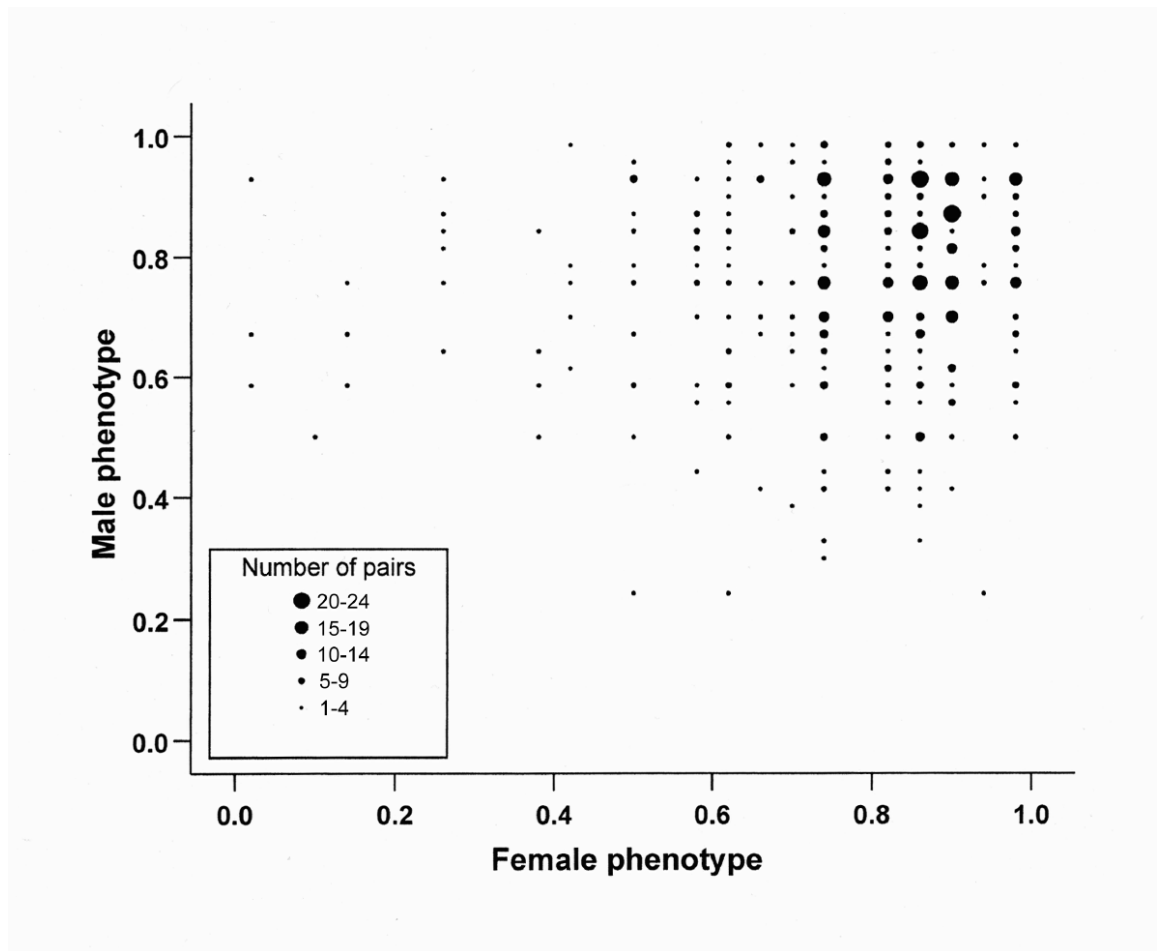


Figure 2.1 Males and females of mated pairs at Riske Creek showed positive assortative mating for phenotype using HI1. A phenotype of 0 is a pure yellow-shafted flicker while 1 is a pure red-shafted flicker. Many points include multiple pairs as indicated by the legend.

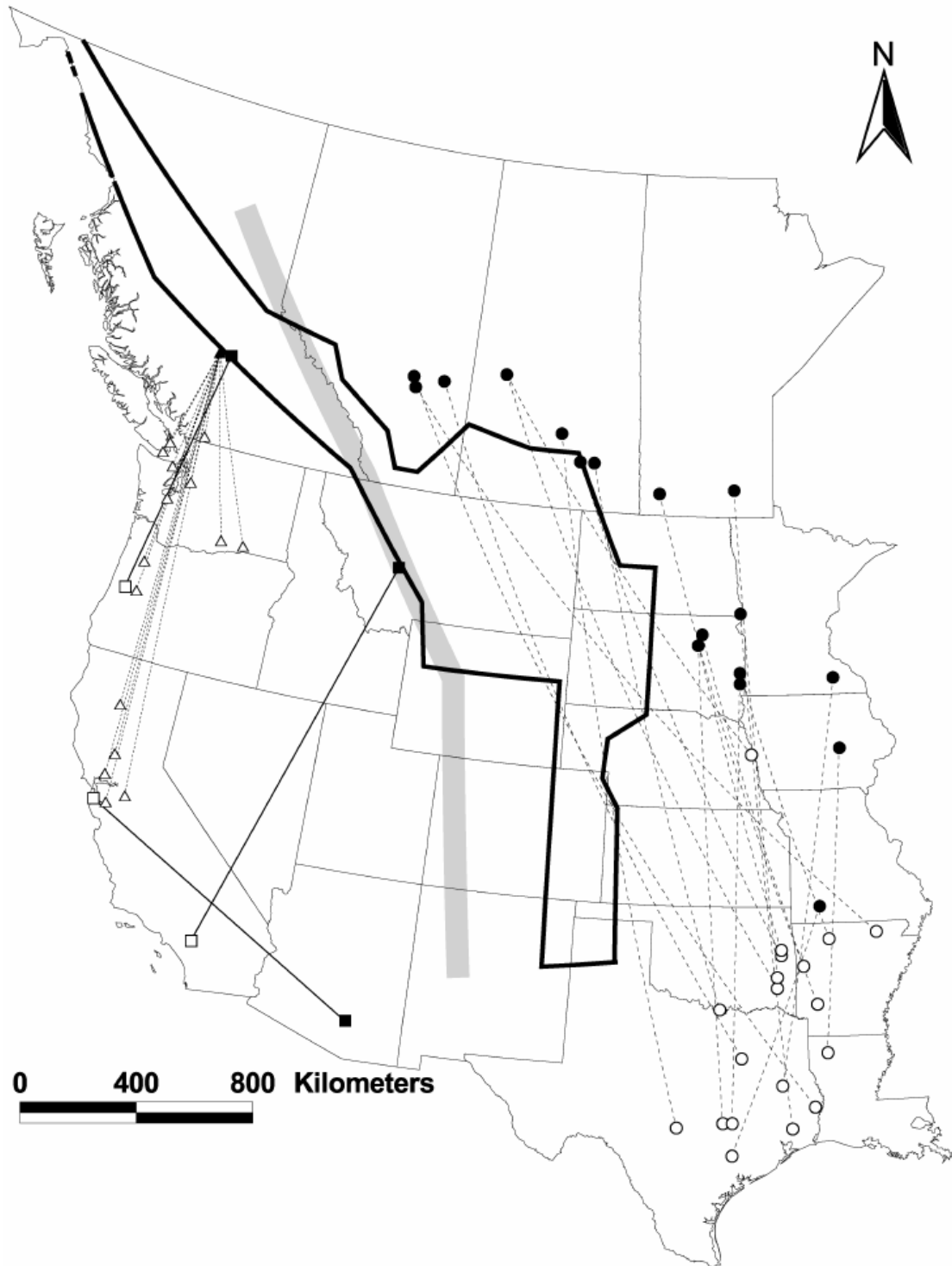


Figure 2.2 Breeding (filled symbols) and wintering (empty symbols) locations for migratory yellow-shafted (circles), hybrid (triangles) and red-shafted flickers (squares) in western North America. The hybrid zone outlined in black is the 20% and 80% transition contours for eastern yellow-shafted flickers and western red-shafted flickers (Moore 1995). The grey line running northwest-southeast is the rocky mountain belt.

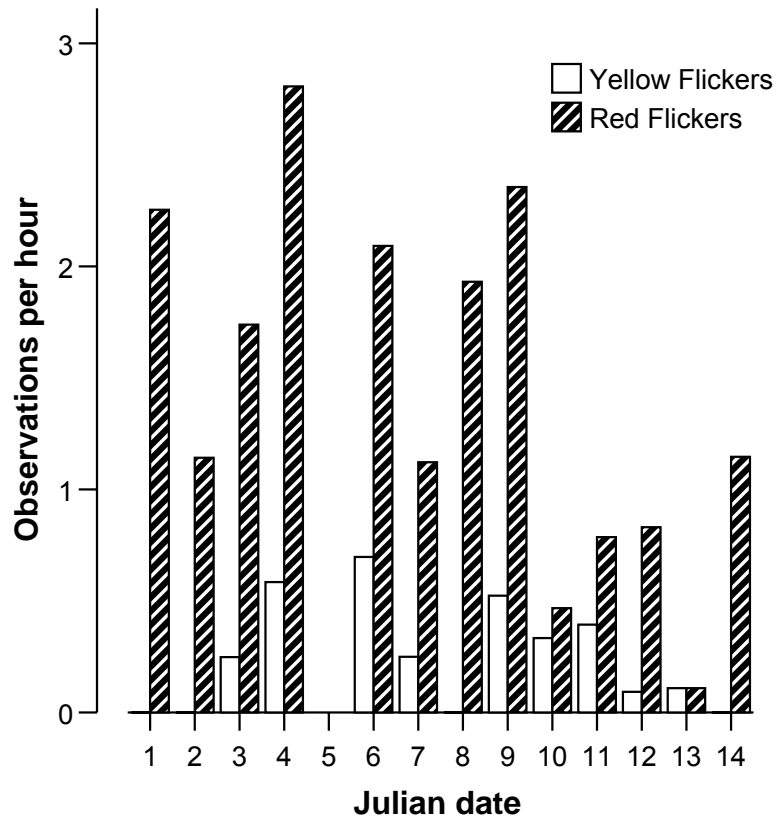


Figure 2.3 Observation rates of newly-arrived individuals to Riske Creek in 2006. For clarity, individuals that were hybrid were excluded and only extreme red and yellow phenotypes were plotted. Because observation time per day varied sightings are standardized by dividing daily sightings by observation time. Julian date 1 is April 17.

colour forms in 2006 (two-sample Kolmogorov-Smirnov test: $Z = 0.45$, $P = 0.99$; Fig. 2.3). Date of first egg was significantly affected by year (males: $F_{8,722} = 8.56$, $P < 0.001$; females: $F_{8,719} = 9.57$, $P < 0.001$) and parental age (males: $F_{2,722} = 29.45$, $P < 0.001$; females: $F_{2,719} = 25.54$, $P < 0.001$), but not HI1 (males: $F_{2,722} = 0.91$, $P = 0.40$; females: $F_{2,719} = 1.21$, $P = 0.30$).

2.3.4 Annual variation in patterns of assortative mating and weather

While assortative pairing according to HI1 was significant and positive with the years pooled (see above), there were no significant relationships with the nine years considered individually. Furthermore, the direction of the correlations varied from positive in some years to negative in others. Regional April temperatures from Seattle negatively correlated with mean nest initiation date on my study area suggesting that weather did influence breeding phenology ($r = -0.79$, $P = 0.011$, $n = 9$). April temperatures in Seattle correlated with the proportion of yellow flickers on the study area ($r = 0.75$, $P = 0.02$, $n = 9$) and with the annual mean HI1 in the population ($r = -0.66$, $P = 0.056$, $n = 9$).

NAO but not PNA correlated with the mean HI1 of flickers in my population in a given year (NAO: $r = 0.80$, $P = 0.01$, $n = 9$; PNA: $r = -0.26$, $P = 0.49$, $n = 9$). In particular, there were more *auratus*-type birds in years with low index values (Fig. 2.4). Although mean HI1 was correlated with the proportion of yellow birds in my population ($r = -0.80$, $p = 0.01$, $n = 9$), it was not clear that the movement of yellow individuals from eastern areas of the continent was the mechanism driving the relationship with the NAO as it did not correlate with the annual proportion of yellow flickers at Riske Creek ($r = -0.50$, $P = 0.17$, $n = 9$).

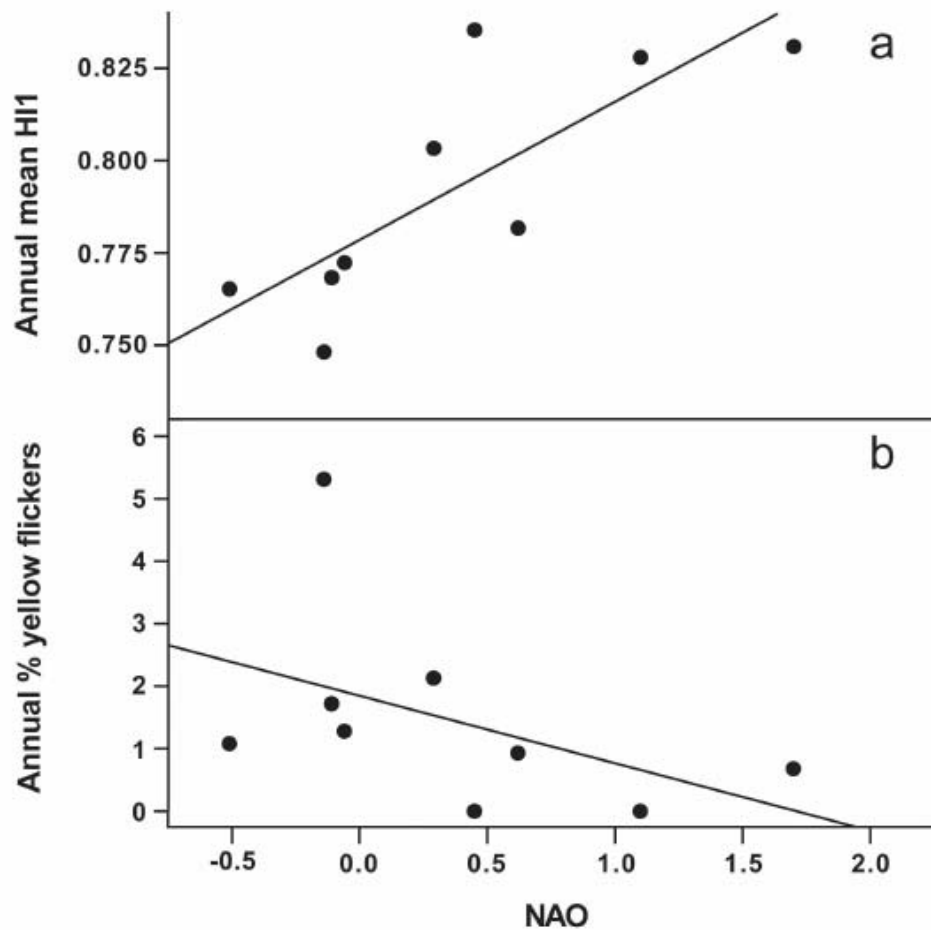


Figure 2.4 Relationships between the North Atlantic Oscillation (NAO) and (a) average annual phenotype, and (b) annual proportion of yellow (*auratus*-type) flickers breeding at Riske Creek. Each point represents between 50 and 120 nests.

2.4 Discussion

In the pooled dataset collected over nine years, there were weak, but significant, patterns of positive assortative mating within pairs of hybrid flickers at Riske Creek consistent with Wiebe (2000). Pairing is reported to be random in the southern part of the hybrid zone (Short 1965; Bock 1971; Moore 1987) but small samples in some of those studies may limit the ability to detect trends. Assortative pairing or the lack of it is not a critical prediction of the BSHS, but according to this idea, hybrids have the greatest fitness in the hybrid zone and so the best strategy may, in fact, be disassortative pairing in the hybrid zone in order to produce hybrid offspring (Moore 1977). Without carefully controlled experiments of mate choice in a laboratory setting, active choice in flickers based on plumage or other attributes can not be excluded, although there is currently no evidence for it.

2.4.1 *Possible influence of migration and wintering location on hybrid zone dynamics*

Evidence that assortative mating in my population was passive and driven by different migration patterns is still equivocal. Migratory yellow-shafted and red-shafted flicker populations seem to winter in the eastern and western United States respectively, while reddish-orange hybrids at Riske Creek migrated to wintering areas along the west coast south to California. The lack of band recoveries of *auratus*-type hybrids from my population and the scarcity of reports of hybrid flickers from banding stations generally means that it is still unknown whether different phenotypes of hybrids migrate along different routes or segregate in different wintering areas. I was unable to detect a difference in arrival times between phenotypes at Riske Creek in 2006, or a difference in date of first egg according to phenotype in the larger dataset. Casual observations in

early spring in previous years confirm that arrival times of reddish and yellowish birds are never completely segregated, but this does not exclude the possibility that significant differences in arrival times may occur in some years, depending on weather patterns. Furthermore, there is substantial variation in laying dates not accounted for by arrival time, so nest initiation may be a too coarse measure to detect differences in arrival that may only vary by a few days.

Although direct evidence of different arrival times was lacking, regional and continental weather patterns were correlated to annual variation in phenotypes. As expected, higher April temperatures in Seattle were linked to earlier egg-laying dates in the population at Riske Creek as a whole, suggesting that benign weather in the Pacific Northwest in spring generally accelerates arrival. Interestingly, the NAO correlated, at least weakly, with the average annual phenotype on my study area. One explanation is that the NAO influences the distance that *auratus* individuals migrate from the east, and this influences the annual influx of yellowish adults into my population, but I did not find a significant correlation between NAO and the proportion of yellow flickers. However, in all these relationships, the sample size was small (nine years) and so more information is needed to elucidate the exact mechanisms of how weather patterns influence the large-scale movements of different populations of migrating flickers.

It is important to recognize that NAO influences not only proportions of certain phenotypes breeding in the hybrid zone, but also that it may influence flickers throughout their annual cycle. Nott et al. (2002) found strong relationships between positive winter NAO conditions and higher insect abundance that in turn increased reproductive success in several temperate migrants breeding in the Pacific Northwest. Winter NAO therefore seems to influence weather patterns in the Pacific Northwest and

eastern North America in a similar manner. Therefore, if the majority of flickers in my study population migrate through the Pacific Northwest, the NAO may influence migration, as suggested here, but also reproduction and survival. Analyses of reproductive success and survival should therefore look at these relationships when discerning fitness differences between phenotypes.

Annual variation in phenotypes has implications for the dynamics of hybrid zones. While studies in the south suggest that the flicker hybrid zone has been stable at least for centuries (Rising 1983; Moore and Buchanan 1985), evidence from northern populations suggests there may be increasing introgression (McGillivray and Biermann 1987). A time-series long enough to detect a directional shift in the hybrid zone is unavailable at Riske Creek, but here the distribution of phenotypes fluctuates annually apparently in response to large-scale weather patterns. Wiebe and Bortolotti (2001) argued that the complex mountainous topography in British Columbia may not produce the smooth and continuous environmental clines hypothesized to keep the subspecies separate in the United States. Instead, weather and migratory movements may determine the proportion of phenotypes that breed in different geographic locations in the north.

Since assortative mating is a mechanism of premating reproductive isolation, it will act as a barrier to introgression regardless of the subsequent reproductive performance of the pair (Coyne and Orr 2004). However, it is unlikely that the overall weak assortative pairing at Riske Creek is a major force of reproductive isolation even in my northern population. Further data on reproductive performance of breeding pairs according to their phenotypes is needed to determine if any reproductive isolation occurs at later stages of breeding as this can be another mechanism that prevents introgression and keeps hybrid zones stable (Moore 1987).

The role of seasonal migration in determining the dynamics of hybrid zones in birds is a new area of study but there are a few other examples of how movements on the landscape affect the interbreeding of different populations. Hybridization opportunities between red-breasted (*Sphyrapicus ruber*) and red-naped (*S. nuchalis*) sapsuckers, which occur and hybridize at Riske Creek, are likely further reduced because of differences in arrival to breeding sites (Howell 1953; Johnson and Johnson 1985). In Europe, two subspecies of willow warblers (*Phylloscopus trochilus trochilus* and *P. t. acredula*) that breed in Scandinavia migrate to either southern or western Africa depending on their breeding latitude (Chamberlain et al. 2000; Bensch et al. 2006). It is assumed that populations pair assortatively because there is a two week difference in arrival times between them (Bensch et al. 1999). This leads to reduced gene flow and a low production of hybrids, resulting in traits diverging quickly between the populations (Bensch et al. 1999). In another example, northern populations of chiffchaffs (*Phylloscopus collybita abietinus*) arrive on the breeding grounds in northern Sweden later than southern populations (*P. c. collybita*) that breed in southern Sweden because *abietinus* individuals have different migration routes that are hundreds of kilometres longer than *collybita* individuals. It is hypothesized that if these parapatric subspecies expand their ranges and begin to interbreed in a contact zone, *abietinus* individuals that arrive later will be at a selective disadvantage due to poorer body condition and reduced ability to establish or maintain breeding territories (Hansson et al. 2000). If so, different migration schedules drive competitive asymmetry, influencing which subspecies breeds successfully and ultimately may result in a moving hybrid zone. In these examples, migration timing further isolates reproduction of phenotypes in contact zones

characterized by hybrid inferiority, however, hybrid inferiority is not the case with flickers (Moore and Koenig 1986).

As a barrier to introgression, assortative mating influences the degree to which populations diverge. In hybrid zones where individuals migrate from different geographic areas to breeding areas, climatic patterns may result in proportions of phenotypes changing or temporal segregation between phenotypes both of which could result in annually variable pairing arrangements. If hybrids have equal or greater fitness compared to parental forms, assortative mating should only arise through passive mechanisms and over evolutionary time should select for individuals to delay breeding after arrival to obtain a superior mate. Migration can thus influence how gene flow progresses or is impeded in stable hybrid zones.

CHAPTER 3

REPRODUCTIVE PERFORMANCE OF NORTHERN FLICKERS ACCORDING TO PHENOTYPE IN THE NORTHERN PORTION OF THE HYBRID ZONE

3.1 Introduction

When two species interbreed in a hybrid zone, the relative fitness of the species determines the persistence and stability of the zone (Endler 1977; Barton and Hewitt 1985; Hewitt 1988). Some scenarios predict that the hybrid zone will shift over time if one parental type has greater fitness than the other (e.g. fitness asymmetry model; Rohwer and Wood 1998) or that introgression between the two populations will be complete if there are no fitness consequences to hybridization (ephemeral-zone hypothesis via introgression; Dobzhansky 1940). Alternatively, hybrid zones can persist in the same geographic location over hundreds or thousands of generations and therefore be considered stable.

There are three main explanations for stable hybrid zones. The dynamic-equilibrium hypothesis (DEH) predicts that naïve, dispersing parental-type immigrants interbreed in a narrow zone that is sparsely populated (density trough) characterized by reduced hybrid fitness (Barton and Hewitt 1985, 1989). Alternatively, the bounded-hybrid superiority hypothesis (BHS) suggests that hybrids have greater fitness than parental types in the hybrid zone as dictated by ecological selection gradients within the zone of contact (Moore 1977). The selection-hybridization hypothesis suggests that the fitness of hybrids relative to parental types varies over time depending on fluctuating selection

pressures such as variable environmental or ecological factors (e.g. climate).

Hybridization therefore occurs regularly but at low levels (Grant and Grant 1992, 1993; Bell 1997). Fitness is therefore the primary measure to distinguish between hypotheses for hybrid zones.

Differences in surrogate fitness measurements may be observed at any part of the annual cycle but most studies focus on reproductive performance. For example, hybridization may result in greater infertility, embryonic mortality, developmental abnormalities or incompatible behaviour such that fewer hybrid offspring are produced or survive (Kruuk et al. 1999). Sometimes reproductive problems are observed in the F2 generation when hybrid offspring themselves attempt to reproduce (Lanyon 1979; Veen et al. 2001). If there are no obvious signs of inviability of hybrids, then comparing the reproductive performance of phenotypes in a hybrid zone should provide insight into how the zone is maintained and the potential for hybrid zone movement.

The northern flicker hybrid zone has been known to ornithologists for at least 150 years (Allen 1892; Deakin 1936). The zone is considered stable and, because a study failed to detect reduced fitness associated with hybridization (Moore and Koenig 1986), the BSHS is the leading hypothesis to explain the maintenance of the zone (Moore and Buchanan 1985; Moore and Price 1993). However, this previous research was conducted in the southern portion of the hybrid zone where dynamics may differ from the north where flickers are migratory. Furthermore, previous measures of reproductive performance of hybrid flickers have suffered from small sample sizes and the inability to control for factors associated with reproductive output such as parental age and seasonal timing (e.g. Smith et al. 2006). Flickers are an excellent model to test for selection

against hybrids or mixed pairs because mate choice does not seem to be strongly influenced by phenotype (Bock 1971; Moore 1987; Wiebe 2000).

To measure fitness in a hybrid zone it would be ideal to follow individuals of known parentage (i.e. pedigrees) through their lives and monitor their lifetime reproductive success and the success of their offspring (Grant and Grant 1992). However, this is usually difficult or impossible in open populations and so individual fitness is estimated using surrogates such as reproductive success (Grant and Grant 2000). Reproductive success for birds is often measured by one or two simple parameters such as clutch size or number of fledglings but for a better idea of possible mechanisms responsible for any fitness differences, it is important to quantify reproduction at several stages.

Behavioural dominance may influence the ability to defend a territory and retain a mate that could ultimately be the main determinant of reproductive potential. For example, golden-winged warblers (*Vermivora chrysoptera*) experimentally altered to appear as hybrids were unable to maintain territories or retain mates (Leichty and Grier 2006). In another example, the introgression of Carolina chickadee (*Poecile carolinensis*) genes into the range of pure black-capped chickadee (*P. atricapillus*) genes appears to be driven by both behavioural dominance of Carolina males over black-capped males and female preference for these dominant Carolina males (Bronson et al. 2003b; Reudink et al. 2006, 2007) despite the reduced reproductive success of mixed pairs (Bronson et al. 2005).

Differences in behavioural dominance could affect reproductive success by reducing breeding potential for certain phenotypes, which may not be apparent if subsequent measures of reproductive success are similar between forms. Territory turnover can be observed by monitoring potential breeding sites and the phenotypes of the individuals

occupying those sites over time. Dominance of hybrid individuals is often determined by comparing measures of aggression against experimentally presented models with different phenotypes (e.g. Pearson and Rohwer 2000; McDonald et al. 2001). If one phenotype is inherently more likely to win encounters, this could occur because it reacts more aggressively against the other phenotype compared to its own phenotype. Alternatively, the aggression level of one phenotype may be consistent across all phenotypes of opponents, but the other phenotype may consistently avoid agonistic interactions by retreating.

In this chapter, I focus on the relationship between phenotype and reproductive success of northern flickers within the hybrid zone. I examined several reproductive parameters including territory retention, aggression level towards conspecifics, laying initiation date, clutch size, hatching success and fledging success. My objective was to test for differences in performance among phenotypes.

3.2 Methods

Flicker territories were monitored by the method outlined in section 1.4.2 and the phenotypes of individuals and pairs were recorded as in section 1.4.3.

3.2.1 Territory maintenance and aggression

Both males and females defend mates and breeding territories such that aggressive behaviours are not limited to a single sex. In spring during territory establishment, flickers often have wicka-dance contests where participants face each other with heads raised and have “mock” fencing duels using their bills (Moore 1995). The undersides of the wings and tails are flicked during such encounters and are visible to the opponent. Wicka-dances can last several hours at a time although there are usually breaks between bill fencing duels at which time the combatants will commonly chase each other through

the trees. While the exact purpose of wicka-dances is unknown, it is thought to play a role in both mate choice and territory defence (Moore 1995). I monitored territory turnover and intrasexual agonistic displays and interactions (wicka-dances and chases) of flickers during 2005 and 2006. Starting shortly after birds arrived on the study area after migration (last two weeks of April), I censused breeding territories using tape-recorded territorial calls and recorded the general phenotype (red, orange, yellow; nape patch or no nape patch) of individuals responding in breeding territories. A given territory was revisited, on average, every four or five days for two weeks. A territory turnover occurred when a bird with a different phenotype was observed subsequently on a given territory. If two individuals were detected on a territory, I recorded both, and then considered the phenotype that remained on the territory, or was trapped at the nest in a subsequent visit, as the winner. For agonistic interactions, I recorded which phenotype was the aggressor. I recorded both male-male and female-female interactions and pooled observations over both years because of small sample sizes. I used binomial tests ($P = 0.5$) to determine if certain phenotypes won more contests than expected by chance; if there are no differences in territory turnover rates based on phenotype, then each colour should win as many interactions as it loses.

3.2.2 Experimental tests of aggression towards models

I presented a taxidermy model of both a pure yellow-shafted and a pure red-shafted male intruder to yellow and red male territory holders using a paired experimental design. Yellow-shafted models ($n = 2$) had a HI1 = 0 and were obtained from the University of Saskatchewan. Red-shafted models ($n = 2$) had a HI1 = 1 and were obtained from the University of British Columbia. I chose territory holders that were phenotypically as pure yellow- or red-shafted as possible but pure yellow-shafted

flickers were rare. Still, the chosen yellow males all had yellow rectrices and scored in the most yellow 28% (HI3) of the population. The models were prepared in an erect posture with the head turned to one side to display the face and mustache (malar stripe) while the tail and wings were slightly spread to show the conspicuous undersides of the remiges as is common in wicka-dances displays (Moore 1995). The order of model presentations was randomly assigned and separated by at least one day, and the specific model was also randomly chosen.

Flicker nests are occasionally parasitized by other female flickers (K. Wiebe, unpub. data) and members of a territorial pair are likely most aggressive towards intruding individuals during the egg laying period of the nesting cycle. Thus, I conducted the trials early in the egg-laying period when the nest had at least two eggs to increase the chances of flickers responding to intruders. Models were placed on a wooden stake about 1.5 m above the ground and about 5 m in front of the cavity entrance where a returning territorial flicker should see it easily. To make the models more lifelike, I jiggled them slightly with an attached fishing line. A five minute silent period at the beginning of the trial was followed by a five minute territorial call from a tape recorder placed beneath the model. Reactions of the territorial males were observed from a camouflage blind 10-20 m from the cavity entrance. I do not believe the blind inhibited flicker responses because on several occasions territorial males landed less than 2 m from the observers between the model and the blind.

The trial lasted for a maximum of 15 minutes or until the territorial male struck the model. I started to record the "response time" from when I thought the territorial male could see the model and used this time to calculate response rates. I assumed that a more aggressive (and potentially dominant) male would attack more frequently,

approach the model more closely, and show higher rates of calls and agonistic behaviours (Rohwer 1982; Fisher and Wiebe 2006c). I recorded a variety of aggressive calls and responses but because of small sample sizes in each behaviour category, I calculated 'pooled calls' as the sum of peahs, wickas, and whurdles (i.e., territorial vocalizations, Moore 1995) and 'pooled behaviours' as summed calls, tree drums and bill fences. I also recorded whether the territorial male blocked the cavity, whether he struck the model, the minimum distance he approached the model and the mean distance to the model using 30-second intervals. Minimum distance, pooled calls and pooled behaviours were analyzed with nonparametric Wilcoxon signed rank test because they were non-normal. Binary data (cavity blocking and striking model) were analyzed with McNemar change tests (Siegel and Castellan 1988). Mean distance was log-transformed and analyzed with repeated measure ANOVA (Zar 1999).

3.2.3 *Reproductive success*

I checked active cavities with a mirror and flashlight every three to four days to determine nest initiation date (lay date), clutch size and nest success (successful or depredated). For those nests where at least one egg hatched, I calculated hatching success (brood size/clutch size; arcsine transformed) and the number of fledglings.

Reproductive success could vary with the phenotype of either the male or the female, or could be influenced by the degree of phenotypic difference between members of the pair. Therefore, I modelled reproductive success using three types of independent variable (HI): 1) male phenotype and 2) female phenotype or 3) the difference between the HI1 indices within a pair. I also performed analyses on two forms of the hybrid index: a continuous score of several plumage categories (HI1), and a categorical score with individuals as yellow ($HI1 < 0.33$), orange ($0.34 < HI1 < 0.66$), or red ($HI1 > 0.67$).

The difference between the male and female HI was used either as a continuous variable or categorically scored as more ($|\Delta HI| < 0.33$) or less similar ($|\Delta HI| > 0.33$). Because the BSHS suggests the fitness of hybrids may be greater than either parental type and best represented as a quadratic function, I graphed all the data and checked for obvious non-linear trends but none was apparent. Therefore, I used GLM models assuming linear relationships among variables. The GLM models included any factors strongly associated with the dependent variable (e.g. parental age, year, and laying date). Initial models included all two-way interactions but non-significant effects were eliminated in a backward-stepwise procedure to obtain a final model. The continuous HI scores and the categorical HI gave results that were qualitatively identical so I only present the models with the categorical HI.

Hatching success and fledging success had non-normal distributions after arcsine transformation and so I used Kruskal-Wallis tests to compare these variables among the three phenotype categories. Finally, I compared nests successful at fledging at least one nestling and depredated nests (nest success) with a forced-entry logistic regression using the following variables: parental HI index, parental age, and year. As with the GLM models, two-way interaction terms were included initially but deleted if not significant. I tested to see if the data fit the model using Hosmer-Lemeshow GOF tests (Hosmer and Lemeshow 2000). The continuous and categorical HI indices gave similar results so only the model with the categorical HI scores is shown. All tests were two-tailed and considered significant at $\alpha = 0.05$.

3.3 Results

3.3.1 Territory retention and defence levels

Table 3.1 Number of contests (chases and territory turnovers) between pairs of flickers of different phenotypes at Riske Creek, British Columbia observed in 2005 and 2006. *P*-values are from a binomial test ($P = 0.5$) to determine if the winning phenotype won more contests than expected. The phenotype listed first won the majority of contests which is indicated.

Interaction type	<i>n</i>	% contests won	<i>P</i>
Red-orange	25	60	0.42
Yellow-Red	17	59	0.63
Yellow-orange	5	80	0.38

I observed 47 natural aggressive interactions between flickers where I could designate phenotypes and a winner (Table 3.1). Binomial tests with P set to 0.5 suggest each phenotype won as many encounters as it lost (Table 3.1). I presented models to 21 red and 20 yellow territorial males over two summers. Model colour was not associated with the probability of blocking cavities by either red (McNemar test: $P = 0.29$) or yellow ($P = 1.0$) territorial males. Similarly, the rate of striking the model did not depend on model colour for red males ($P = 0.5$) while there was a trend that yellow males struck red models more often than yellow models ($P = 0.07$). With model types pooled, yellow males did not hit models more often than red males ($\chi^2 = 0.4$, $df = 1$, $P = 0.58$). The minimum approach distance did not vary according to model colour for red males ($Z = -1.54$, $P = 0.12$) but yellow males approached red intruders more closely than yellow intruders ($Z = -2.99$, $P = 0.003$).

For mean distance, there was a significant interaction between phenotype of the defending male and model colour ($F_{1,38} = 4.19$, $P = 0.048$; Fig. 3.1) so I examined each phenotype separately. There was no significant difference in distance according to model colour for red males ($t = 0.39$, $df = 20$, $P = 0.70$), but yellow males stayed closer to red models than to yellow models ($t = -3.67$, $df = 18$, $P = 0.002$). Red ($Z = -0.19$, $P = 0.85$) and yellow ($Z = -1.60$, $P = 0.11$) males had similar call rates which did not differ according to model phenotype (Fig. 3.2A). With all agonistic behaviours pooled, red males did not behave differently according to intruder colour ($Z = -1.01$, $P = 0.31$) but yellow males behaved more aggressively towards red intruders ($Z = -1.98$, $P = 0.048$; Fig. 3.2B). The average measure of aggression with model types pooled was not different between red and yellow males ($Z = -1.33$, $P = 0.18$).

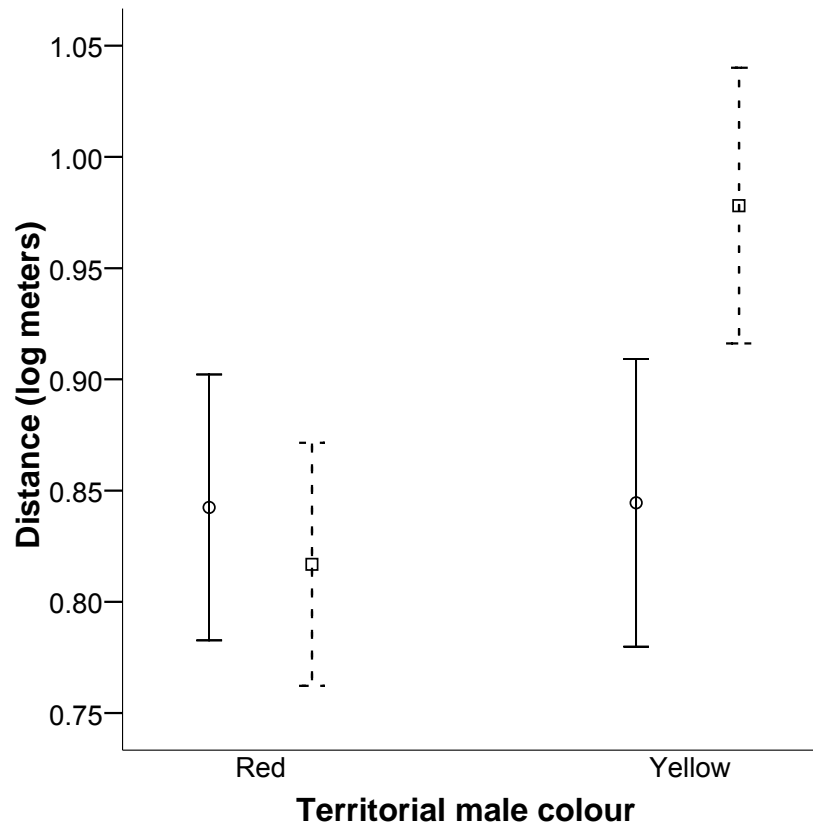


Figure 3.1 Mean (\pm 1SE) distance to red (circles, solid line) or yellow (squares, dashed line) taxidermy models during experimental trials for red or yellow territorial male northern flickers.

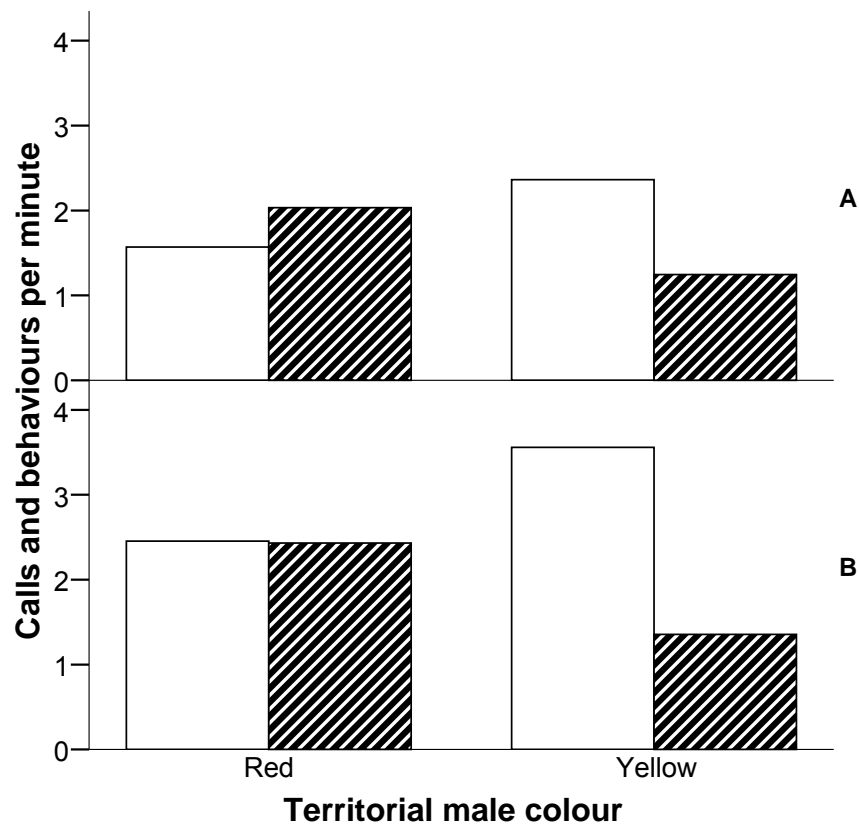


Figure 3.2 Mean call (A) and behaviour (B) rate of territorial male flickers to red (open bars) and yellow (cross-hatched bars) taxidermic models. Pooled behaviours include calls, bill drums and bill fences. Means are shown for illustration, but statistical tests were non-parametric (see text).

3.3.2 *Reproductive success*

A total of 865 breeding attempts where the phenotype of both parents could be determined was monitored between 1998 and 2006 at Riske Creek (Table 3.2). The mean laying date in the population was 13 May and most variation in laying date was explained by parental age and year but not by phenotype of either the male or female parent (Table 3.3). Similarly, laying date was not associated with the difference in HI between members of a pair ($F_{1,678} = 0.76$, $P = 0.38$). With laying date controlled for in the model, neither male nor female phenotype was associated with clutch size (Table 3.3, Fig. 3.3). There was a weak trend that more similar pairs had larger clutches ($F_{1,649} = 3.26$, $P = 0.07$). The probability a nest was successful or depredated was not associated with the male's (Logistic Regression: Wald = 2.91, df = 2, $P = 0.23$) or the female's phenotype (Wald = 5.02, df = 2, $P = 0.08$) nor the difference in pair phenotype (Wald = 0.01, df = 1, $P = 0.93$).

Considering only nests that did not fail, hatching success was generally between 80-90% of the clutch (Fig 3.4). I found no difference in hatching success between phenotypes for males ($\chi^2 = 3.00$, df = 2, $P = 0.22$), females ($\chi^2 = 4.76$, df = 2, $P = 0.09$) or pairs ($\chi^2 = 0.39$, df = 1, $P = 0.53$). Comparing the fraction of hatched nestlings that fledged (fledging success), there was a trend that yellow males had higher fledging success than other phenotypes ($\chi^2 = 5.61$, df = 2, $P = 0.06$; Fig 3.4) but fledging success did not differ for females ($\chi^2 = 0.19$, df = 2, $P = 0.91$) or pairs ($\chi^2 = 0.12$, df = 1, $P = 0.73$). At the end of the brood-rearing period, there was no difference in the number of fledglings according to phenotype of either parent (Table 3.3, Fig. 3.3) or the difference between members of a pair ($F_{1,547} = 0.01$, $P = 0.93$).

Table 3.2 Descriptive statistics mean \pm SD (n) for pairs of flickers at Riske Creek, British Columbia 1998-2006. Laying date is Julian date and includes only first nesting attempts. All columns exclude nests that did not hatch at least one egg except for breeding success which is the number of fledglings produced divided by clutch size in both successful and failed nests. Sample sizes differ for comparisons because not all information was collected at each nest. Phenotype categories are based on a Hybrid Index (HI1) score as outlined in text. There were no yellow-yellow pairs.

Phenotype		Laying date	Clutch size	Brood size	# of Fledglings	Breeding success
Male	Female					
Red	Red	133 \pm 8.5 (405)	7.9 \pm 1.5 (468)	6.9 \pm 1.6 (466)	6.0 \pm 1.9 (471)	0.66 \pm 0.35 (549)
Red	Orange	135 \pm 9.1 (44)	8.1 \pm 1.4 (52)	6.9 \pm 1.5 (53)	5.9 \pm 2.2 (54)	0.60 \pm 0.35 (62)
Red	Yellow	135 \pm 8.6 (9)	8.2 \pm 2.0 (9)	7.1 \pm 1.6 (9)	6.4 \pm 1.2 (9)	0.66 \pm 0.36 (11)
Orange	Red	132 \pm 7.9 (82)	8.1 \pm 1.5 (90)	7.0 \pm 1.6 (88)	6.1 \pm 1.8 (93)	0.67 \pm 0.31 (102)
Orange	Orange	132 \pm 6.8 (17)	8.1 \pm 1.7 (21)	6.7 \pm 1.7 (21)	5.7 \pm 2.3 (21)	0.60 \pm 0.36 (25)
Orange	Yellow	131 \pm 6.3 (5)	7.0 \pm 1.0 (5)	6.0 \pm 1.2 (5)	5.2 \pm 2.2 (5)	0.74 \pm 0.31 (5)
Yellow	Red	131 \pm 8.3 (6)	7.4 \pm 0.9 (8)	6.3 \pm 1.5 (8)	5.9 \pm 1.1 (7)	0.72 \pm 0.31 (8)
Yellow	Orange	126 \pm 2.8 (2)	7.5 \pm 0.7 (2)	6.5 \pm 2.1 (2)	6.5 \pm 2.1 (2)	0.86 \pm 0.20 (2)
Mean		133 \pm 8.4 (570)	7.9 \pm 1.5 (655)	6.9 \pm 1.6 (652)	6.0 \pm 1.9 (662)	0.65 \pm 0.34 (764)

Table 3.3 ANCOVA models for various reproductive parameters of northern flickers in the hybrid zone at Riske Creek, British Columbia. Data are from 865 reproductive attempts monitored from 1998-2006. HI refers to a hybrid index calculated as yellow, orange or red (see methods). Only first nesting attempts are included.

Variable, Source	df	MS	F	P
Laying date				
Male HI	2	47.28	0.87	0.42
Female HI	2	18.48	0.34	0.71
Male age	2	636.41	11.77	<0.001
Female age	2	390.80	7.23	0.001
Male age * Female age	4	236.86	4.38	0.002
Year	8	452.66	8.37	<0.001
Error	675	54.09		
Clutch size				
Male HI	2	0.75	0.45	0.64
Female HI	2	2.11	1.27	0.28
Male age	2	7.37	4.44	0.012
Female age	2	4.04	2.43	0.089
Year	8	7.88	4.75	<0.001
Laying date	1	185.79	111.95	<0.001
Error	646	1.66		
Fledglings				
Male HI	2	0.06	0.02	0.98
Female HI	2	3.35	0.98	0.38
Male age	2	5.73	1.68	0.19
Female age	2	2.91	0.85	0.43
Year	8	5.48	1.60	0.12
Lay date	1	94.14	27.53	<0.001
Error	544	3.42		

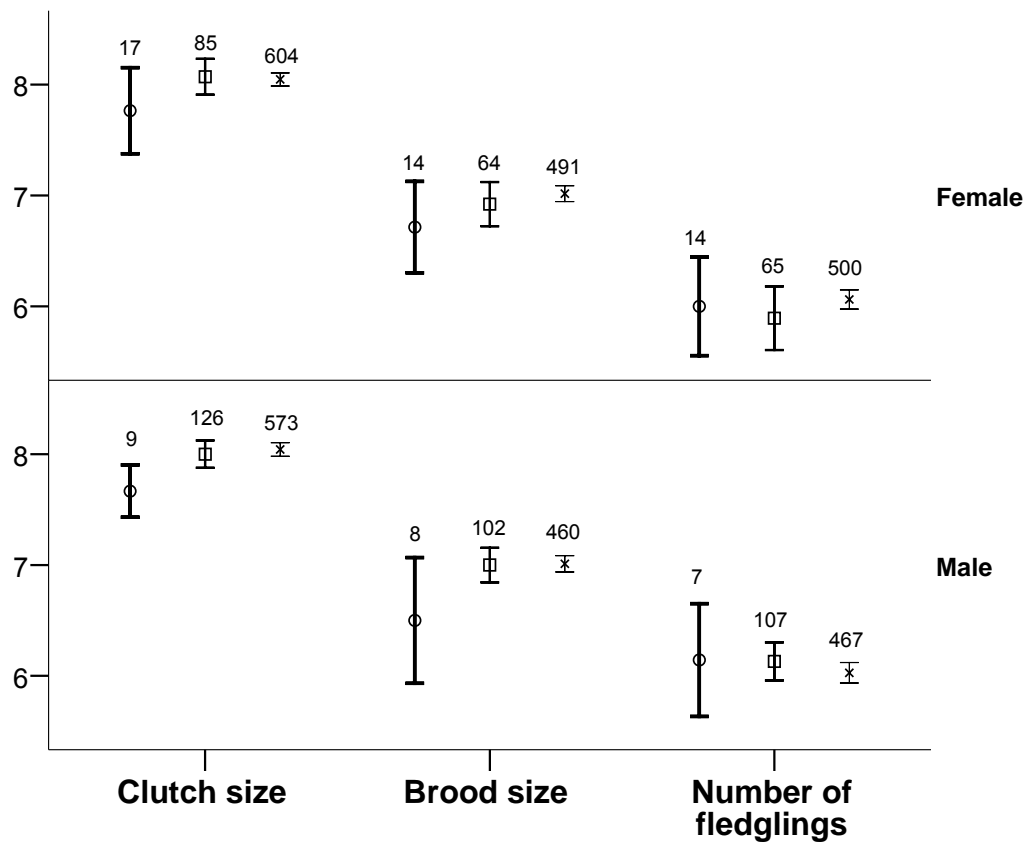


Figure 3.3 Mean \pm 1 SE of clutch size, brood size and number of fledglings for male and female flickers classified as yellow (circles, thick bar), orange (squares, medium bar), or red (star, thin bar). See text for phenotype designations. Numbers above error bars are sample sizes. Clutch size includes all first nesting attempts while brood size and number of fledglings include only nests that hatched at least 1 egg.

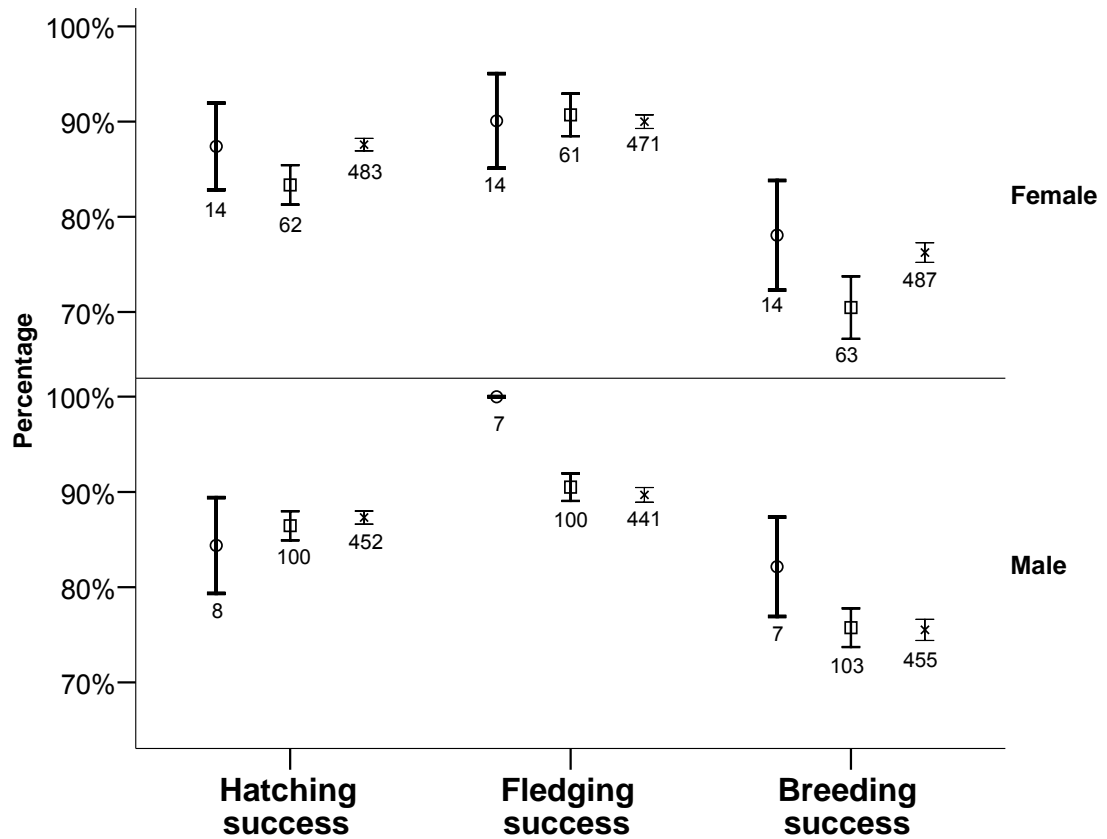


Figure 3.4 Mean \pm 1 SE of hatching success, fledging success and breeding success for male and female flickers classified as yellow (circles, thick bar), orange (squares, medium bar), or red (star, thin bar). Hatching success is the brood size divided by the clutch size and excludes failed nests. Fledging success is the number of fledglings divided by the brood size at hatching and excludes nests that failed to produce any fledglings. Breeding success is the number of fledglings divided by the clutch size and includes all nesting attempts and all nest outcomes. Sample sizes are below bars.

3.4 Discussion

3.4.1 Aggression and territory turnover

Among flickers in the hybrid zone in central British Columbia, phenotype was not associated with the ability to hold a territory, to obtain a mate or to win an aggressive encounter. In fact, the BSHS predicts that hybrids may be more successful, yet orange flickers tended to lose most contests (Table 3.1). Red flickers did not behave differently against taxidermic models of different colours for any measure of aggression but yellow males showed slightly more pooled agonistic behaviours to red models than to yellow ones (Fig. 3.2b). Nevertheless, overall aggression against models of both types was similar for yellow and red flickers and suggests that one form is not more dominant. If anything, red-shafted (*cafer*) genes are moving into the range of *auratus* east of my study area (McGillivray & Biermann 1987). In the future, it would be useful to replicate the model presentations in the core geographic ranges of both parental types and the *auratus*-dominated portion of the hybrid zone to see if differences in responses to phenotypes may be learned and based on the frequency of contacting different phenotypes.

Introgression that promotes one phenotype can occur through male dominance, or female choice resulting in greater reproductive success of individuals possessing certain genes (Brodsky et al. 1988; Pearson 2000; McDonald et al. 2001; Bronson et al. 2003b; Stein and Uy 2006). Behavioural differences within hybridizing populations during early stages of mate choice and territory establishment are common in moving hybrid zones (Pearson 2000; Bronson et al. 2003b; Leichty and Grier 2006). My results of a lack of differential dominance among males together with a lack of evidence for active mate choice (see chapter 2) suggest that the position of the flicker hybrid zone will not

shift in relation to differential mating opportunities for the phenotypes. In contrast, Pearson and Rohwer (2000) demonstrated that male Townsends warblers (*Dendroica townsendi*) are dominant over male hermit warblers (*D. occidentalis*) and so the hybrid zone is moving and the range of hermit warblers is shrinking. Furthermore, females of both species seem to prefer Townsends phenotypes, and therefore Townsend genes should proceed to fixation across the zone (Pearson 2000). McDonald et al. (2001) found that hybrid manakins (*Manacus candei* and *M. vitellinus*) were more aggressive than either parental type. At one site where both hybrids and pure forms were found, hybrids received more reproductive opportunities but some form of counter-selection against hybrids appears to be restricting the further introgression of genes outside the zone and preventing the fusion of both species into hybrids (Stein and Uy 2006).

3.4.2 Reproductive success and hybrid fitness

At least at the time of fledging, no significant differences in reproductive performance according to phenotype was found for either males or females and there was no suggestion that dissimilar pairs performed less well than similar pairs. This agrees with other studies of flicker reproduction (Short 1965; Moore and Koenig 1986) and provides evidence against the DEH. Coupled with the prediction of reduced hybrid fitness, the DEH also predicts that the hybrid zone corresponds with a density trough because the hybrid zone is in poor quality habitat and hybrids have the lowest fitness (Barton and Hewitt 1989). No density trough is apparent in the southern portion of the zone (Moore and Buchanan 1985) however this prediction has not been tested in the northern portion of the hybrid zone. Breeding Bird Survey (BBS; <http://www.mbr-pwrc.usgs.gov/bbs/>) data suggests that flicker densities are at their highest in British Columbia near Riske Creek and there is no obvious reduction in breeding densities that

correspond with the location of the hybrid zone. These results collaboratively suggest that the DEH does not explain the flicker hybrid zone.

On the other hand, there was no evidence that hybrids performed better than parental types in the hybrid zone. Phenotype did not affect clutch size or the probability of choosing a nest that was not depredated. Hatching success, a result of egg fertility and incubation patterns, was not affected by phenotype and parents raised offspring equally as well. It is still possible, but unlikely, that mortality in the post-fledging period could cause more hybrids than parental types to recruit into the local population. However, my results generally fail to support the BSH which predicts hybrids should have consistently higher fitness than parental forms within the hybrid zone. Sample sizes of pure yellow phenotypes were small at Riske Creek, but no trends were detected even among the orange-red phenotypes where the ability to control for age and year effects were strong. Instead, the models showed that parental age, seasonal timing, and annual variation explained reproductive performance (Table 3.3).

The BSH suggests that fitness of different phenotypes depends on environmental gradients across the hybrid zone such as temperature, evapotranspiration rates, and precipitation, either directly or through adaptations to vegetation communities that are determined by climate variables (Moore and Price 1993). There are several avian hybrid zones in the great plains including flickers (Remington 1968; Swenson and Howard 2004; Swenson 2006) suggesting some form of environmental gradient-based selection (exogenous selection) linked to geographic changes from the hot, dry west to the cool, moist east (Moore and Price 1993). However, Wiebe and Bortolotti (2001) suggested that the northern portion of the flicker hybrid zone in British Columbia, with complex intermountain habitats, likely does not correspond to a similar smooth environmental

gradient that is characteristic of the southern portions of the zone. Thus it is unknown if, or how, exogenous selection operates in the north. Reciprocal introductions of pure and hybrid forms into different environmental settings across the contact zone is a strong way to test between selection caused by genetic incompatibilities (endogenous selection) or environmental gradients that select against certain genotypes (exogenous selection; Arnold and Hodges 1995; Bronson et al. 2003a). Bronson et al. (2003a) took this approach in a moving hybrid zone of chickadees and found reduced hatching success among hybrids due to endogenous effects. However, a similar transplant experiment would be difficult for flickers which are not resident.

Similar to the BSHS, the selection-hybridization hypothesis predicts that hybrid fitness is regulated by environmental factors but that stochasticity causes selection pressures on phenotypes at any location to vary from year to year (Grant and Grant 1992; Bell 1997). Pooling years of data may therefore obscure a relationship between phenotype and success but I did not find any year * phenotype interaction effects in any analyses. However, nine years of data may not be sufficient to detect subtle shifts in selection associated with variable weather patterns.

3.4.3 Explaining dynamics of the hybrid zone in the north

Aspects of the hybrid zone in the north still remain a puzzle and are complicated because individuals are migratory, not resident. Long-term data on distributions of phenotypes in British Columbia and Alaska are lacking, so it is uncertain whether the zone is completely stable or is moving slowly. No differences in reproductive success among phenotypes suggests no barriers to gene introgression and that the hybrid zone should widen; however, the survival of flicker phenotypes during the entire annual cycle still needs to be determined. For example, studies of hybridization in Darwin's finches

(*Geospiza*) found no difference in reproductive success between hybrid and pure pairings but that the survival of hybrids was higher than pure parental types during times of food shortages (Grant and Grant 1992). For flickers, it is unknown whether phenotypes vary their overwintering location or experience different mortality outside of the breeding season associated with weather events that could cause random or cyclic selection patterns for certain phenotypes (e.g. Gibbs and Grant 1987).

To understand individual variability in fitness among populations, we require information on all parts of the annual cycle that may subsequently affect survival, reproduction or recruitment rates (Webster et al. 2004). For migratory populations this information is particularly important because reproductive success may be influenced by activities on the wintering grounds that are hundreds or thousands of kilometres away from the breeding grounds. For example, American redstarts (*Setophaga ruticilla*) that occupy high quality winter territories show earlier arrival date and increased body condition at the breeding grounds (Marra et al. 1998). Birds arriving earlier to the breeding grounds subsequently have higher reproductive success compared to birds that arrive later to the breeding grounds (Norris et al. 2004). While I found no differences in reproductive success among yellow, orange and red flickers, carry-over effects from migratory distance, availability of food resources during winter or other factors may influence reproductive potential more than an individual's phenotype.

It is possible the BHSH explains why the hybrid zone in the south is stable and why gene introgression is limited in much of North America, but that the hypothesis breaks down in northern regions with complex topography and migratory individuals. In the north, annual variation in weather and migratory patterns may cause the hybrid zone to vary somewhat unpredictably in width and location from year to year. If annual weather

variability influences selection then the selection-hybridization hypothesis could apply to the hybrid zone in the north.

CHAPTER 4

SURVIVAL AND LOCAL RECRUITMENT WITHIN THE NORTHERN FLICKER HYBRID ZONE

4.1 Introduction

Patterns of survival, reproduction and dispersal of individuals across a hybrid zone determine whether the zone is stable or moving. Stable hybrid zones may exist although there is selection against hybrids because naïve parental forms continually immigrate into the zone and interbreed (the dynamic-equilibrium hypothesis; Barton and Hewitt 1985, 1989). Alternatively, the bounded-hybrid superiority hypothesis (BHSB) predicts that hybrids have the highest fitness relative to parental forms within the contact zone (Moore 1977) but the zone is maintained by ecological selection gradients such that phenotypes have maximum fitness within the habitat that they are best adapted for (Moore and Price 1993). To distinguish between these two hypotheses, the fitness of hybrids relative to parental types must be assessed to determine how selection operates in the zone (Arnold and Hodges 1995).

Lifetime reproductive success increases with the productivity of a certain reproductive event and/or by surviving to breed over many years (Grant and Grant 2000). Where phenotypes do not differ in annual reproductive success, differences in survival could still affect lifetime success and could have impacts on hybrid zone stability, rate of introgression and hybrid fitness. In relatively short-lived species and

where breeding is annual, surviving even one or two years may double or triple the number of breeding attempts and so survival may be the best overall measure of fitness (Grant and Grant 1992, 2000; Crone 2001).

To date, there is little evidence that hybrid northern flickers have either higher or lower reproductive success than pure phenotypes (Moore and Koenig 1986; chapter 3). However, reproductive success has only been measured as numbers of fledglings produced, but there may be differences in fledgling survival after they leave the nest. As well, survival of adults according to phenotype is unknown so there still could be differences in their lifetime reproductive success. For example, while annual reproductive success was similar between hybrid and pure parental individuals, survival was lower in hybrid sapsuckers (*Sphyrapicus*; Trombino 1998) and higher in hybrid Darwin's finches (*Geospiza*; Grant and Grant 1992).

My main objective in this chapter was to calculate the relative survival of northern flicker fledglings and adults according to phenotype. Although it is ideal to track birds with known pedigrees over their entire life span to discern survival rates (Grant and Grant 1992), this is often impossible for migratory species and those which disperse. Instead, survival of hybrids has been inferred from differences in abundances over different life stages (Vamosi et al. 2000; Rohwer 2004; Albert et al. 2006), return rates of marked individuals (Trombino 1998), or experimental evidence of susceptibility to predators (Vamosi and Schluter 2002). Few studies of survival in hybridizing populations have used a hybrid index, but rather have simply categorized individuals as pure or hybrid. Long-term capture-recapture studies allow robust survival estimates to be calculated and recent advances in information theoretic analyses allow one to calculate how specific covariates (i.e. phenotypic hybrid indices) can influence an

individuals' survival (Cam et al. 2002). Although mark-recapture models are powerful, they can not distinguish mortality from permanent emigration (Cilimburg et al. 2002) but several lines of evidence suggest that survival estimates of adult flickers from program MARK models are accurate estimates of true survival (Fisher and Wiebe 2006a). This is not true for fledglings which disperse long distances. For fledglings, differences in local recruitment among phenotypes should reflect differences in mortality assuming the probability of permanent emigration is independent of phenotype.

By using mark-recapture data from a long-term study of hybrid flickers, I wanted to test the prediction that hybrids have either higher (BHSH) or lower (DEH) survival than parental types. My final goal was to test for mortality differences among phenotypes of offspring born on the study site that recruited into the breeding population.

4.2 Methods

See general methods (chapter 1) for details of study area, trapping protocols and calculating the hybrid indices.

4.2.1 Trapping and resighting effort

Each year between 1998 and 2006, the study area was surveyed daily in spring as flickers arrived and settled starting in mid-April until about June when nestlings were hatching. I used tape-recorded territorial calls to solicit responses from flickers that were defending territories. When a flicker responded, I recorded its sex, phenotype, and any colour bands. Other birds were located once their nest site was found.

Most adults that nest on the study area (>95%) are captured and marked with a unique combination of a single aluminum and three colour-bands to allow individual recognition. Fledglings are banded only with a single, numbered aluminum band and so

are easy to recognize as local recruits. Because detection of nests and capture rate of breeding adults is high, I assumed that most unbanded recruits immigrated from off the study area.

4.2.2 *Survival estimates using program MARK*

I used a Cormack-Jolly-Seber capture-recapture model using program MARK to determine apparent survival (Φ) and resighting probability (p) that incorporated individual and cohort (year) level covariates over nine years. I conducted separate survival analyses using two different phenotypic HI as individual covariates. The first used ordinal scores of five plumage traits (HI1; $n = 1117$) while the second used the continuous colour score of an individual flicker's tail feather from a spectrophotometer (HI3; $n = 591$). Not all individuals had feathers sampled so sample size for the second index was smaller. It is assumed that individual covariates are both normally distributed within the population and remain consistent throughout the lifespan of the individual. Scoring of HI1 and HI3 was consistent; individuals showed no differences in HI1 scores both within (paired t-test: $t = -0.24$, $df = 7$, $P = 0.81$) and between breeding seasons (paired t-test: $t = -0.06$, $df = 182$, $P = 0.96$) while HI3 did not change for flickers with tail feathers sampled between years (paired t-test $t = -1.57$, $df = 68$, $P = 0.12$). For flickers sampled more than once I used the HI1 and HI3 score from the initial capture.

Previous analyses suggested small differences in survival between males and females (Fisher and Wiebe 2006a) so I retained sex-dependent variation in my models (Φ_{sex}) in addition to constancy models (Φ). I then modeled survival according to the hybrid index both with linear dependence (Φ_{HI}), and with quadratic dependence (Φ_{HI^2}) since the BSHS and DEH suggest intermediate phenotypes have higher or lower fitness than pure parental types. I included annual weather variation in the form of the North

Atlantic Oscillation index (mean September - April data; Φ_{NAO}) because large scale weather patterns may affect the survival of migratory birds (see chapter 2). Lastly I incorporated linear and quadratic HI relationships in both interactive and additive models of NAO (e.g. Φ_{NAO*HI}) and sex (e.g. $\Phi_{sex+HI2}$). Recapture probability was parameterized to be constant (p_{\cdot}) or show sex (p_{sex}) dependent variation in addition to linear (p_{HI}) and quadratic (p_{HI2}) effects of HI. Therefore, my candidate model list included 13 parameterizations for survival and 4 parameterizations for recapture for a total of 52 models each for both HI1 and HI3.

A necessary first step in model selection is to determine the goodness-of-fit (GOF) of a global model. Program MARK does not allow GOF testing on covariates so I assessed the most parameterized model without covariates ($\Phi_{sex} p_{sex}$). I used the median \hat{c} procedure available in program MARK to determine if the global model fit the assumptions of mark-recapture analysis using 700 simulations (Cooch and White 2007). A variance inflation factor (\hat{c}) of 1 suggests perfect model fit while a \hat{c} between 1 and 3 suggests acceptable fit (Burnham and Anderson 2002).

I used Akaike's information criterion adjusted for overdispersion and small sample size ($QAIC_c$) to determine the most parsimonious model (Burnham and Anderson 2002). I distinguished between competing models using the difference between the model of interest and the best fitting model ($\Delta QAIC_c$). Akaike weights (w_i) determine the relative support of the various effects (e.g. HI) in the candidate set of models (Burnham and Anderson 2002). Models within 2 Akaike units ($\Delta QAIC_c \leq 2$) were considered as competing models and parameter estimates were derived using model averaging (Burnham and Anderson 2002; Cooch and White 2007).

4.2.3 *Local recruitment*

I scored plumage traits of nestlings when they were banded at approximately 20 days old, just prior to fledging. I calculated a HI for each individual as outlined in chapter 1 however when certain plumage traits had not yet developed (e.g. malar patch) those variables were excluded. I tested if the distribution of phenotypes of nestlings that did eventually recruit was different from phenotypes of nestlings that fledged in their particular cohort (year). As well, I increased sample sizes by pooling year types according to positive or negative NAO values (September - April) and again tested if the phenotype of local recruits in those years differed from the phenotypes in the fledging cohort the previous year. All tests were two-sample Kolmogorov-Smirnov tests with α set at 0.05.

4.3 Results

4.3.1 Survival estimates using program MARK

After correcting for over-dispersion (HI1: $\hat{c}=1.29$; HI3: $\hat{c}=1.25$), the top models for both HI1 and HI3 suggested that survival varied annually according to NAO but that there was little effect of sex or HI (Table 4.1). Three of the top six models for HI1 included NAO and in years with positive NAO, which correlate with above average temperatures in eastern North America (Wallace and Gutzler 1981), winter survival was estimated to be lower but error bars did overlap between all years (Fig. 4.1). Resighting probability was best modeled as sex-dependent with males (0.84) more likely to be detected than females (0.81) but differences were slight as there was also some support for constant resighting rates (Table 4.1). Survival estimates of males (HI1: 0.47; HI3: 0.46) and females (HI1: 0.47; HI3: 0.46) between HI1 and HI3 were almost identical. For HI3, several other models were within 2 QAICc units of the most parsimonious

Table 4.1 Top models ($\Delta\text{QAIC}_c \leq 2$) to explain variation in survival (Φ) and resighting (p) probability of northern flickers at Riske Creek, British Columbia. Models for two different hybrid indices are presented (HI1 and HI3) see text for details. The total QAIC_c , difference of QAIC_c of each model relative to the top model (ΔQAIC_c), Akaike model weight (w_i), number of parameters (K) and deviance are presented for each model. The correction for overdispersion was $\hat{c} = 1.29$ for HI1 and $\hat{c} = 1.25$ for HI3.

Model	QAIC_c	ΔQAIC_c	w_i	K	Deviance
HI1					
$\Phi_{\text{NAO}} p_{\text{sex}}$	1712.61	0.00	0.124	4	1704.6
$\Phi_{\text{NAO}} p_{\cdot}$	1712.99	0.38	0.102	3	1707.0
$\Phi_{\cdot} p_{\text{sex}}$	1713.52	0.91	0.079	3	1707.5
$\Phi_{\cdot} p_{\cdot}$	1713.95	1.34	0.063	2	1709.9
$\Phi_{\text{sex}} p_{\cdot}$	1714.13	1.52	0.058	3	1708.1
$\Phi_{\text{NAO+HI}} p_{\text{sex}}$	1714.46	1.85	0.049	5	1704.4
HI3					
$\Phi_{\cdot} p_{\text{HI2}}$	724.78	0.00	0.106	4	716.7
$\Phi_{\text{NAO}} p_{\text{HI2}}$	725.15	0.37	0.088	5	715.0
$\Phi_{\cdot} p_{\cdot}$	725.83	1.05	0.062	2	721.8
$\Phi_{\cdot} p_{\text{sex}}$	726.15	1.37	0.053	3	720.1
$\Phi_{\text{NAO}} p_{\cdot}$	726.18	1.40	0.053	3	720.1
$\Phi_{\text{NAO}} p_{\text{sex}}$	726.57	1.79	0.043	4	718.5
$\Phi_{\text{sex}} p_{\text{HI2}}$	726.71	1.93	0.040	5	716.6
$\Phi_{\cdot} p_{\text{HI}}$	726.76	1.99	0.039	3	720.7
$\Phi_{\text{HI}} p_{\text{HI2}}$	726.78	2.00	0.039	5	716.7

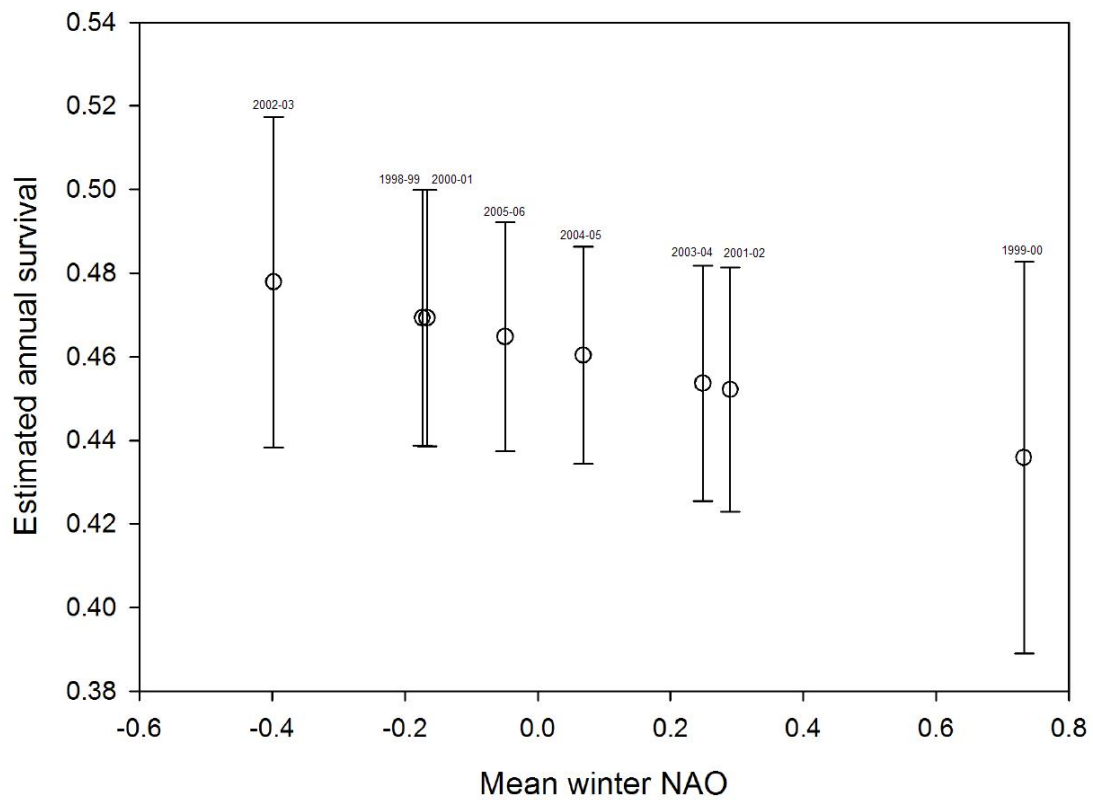


Figure 4.1 Estimated annual winter survival (± 1 SE) of northern flickers from Riske Creek, British Columbia and mean winter North Atlantic Oscillation (NAO) index (September-April) between 1998 and 2006. Survival estimates are for the interval August-April in the years indicated.

model indicating they had some support but, again, survival was best modelled by the annual effects of NAO without sex or HI dependence (Table 4.1). In contrast to HI1, resighting probability was best modelled with a quadratic relationship of HI3 being found in four of the top models.

Although there was no overwhelming evidence that HI greatly influenced survival, I derived survival estimates with regard to HI to better understand the selection pressures operating on the various phenotypes at Riske Creek. Overall, linear relationships of HI held more support (HI1: $w_i = 0.29$; HI3: $w_i = 0.27$) than quadratic relationships (HI1: $w_i = 0.13$; HI3: $w_i = 0.15$). Linear relationships predicted yellow-shafted flickers (HI = 0) had lower survival than red-shafted flickers (HI = 1) whereas quadratic relationships suggested hybrid flickers had the highest survival (Fig. 4.2).

4.3.2 *Phenotypes of recruited nestlings*

A total of 127 of 3501 individuals (3.6 %) born on the study area recruited into the local population between 1998 and 2006. There was no difference between the phenotypes of local recruits compared to the cohort of fledging young both in individual years (all $P > 0.3$) and all years combined (Kolmogorov-Smirnov test: $Z = 0.83$, $P = 0.50$). Because survival was related to NAO (Fig. 4.1), I categorized years as either positive or negative NAO and repeated the analysis comparing phenotypes of the local recruits to the phenotypes of all fledglings in those years but again there were no significant differences (negative NAO years: $Z = 0.58$, $P = 0.90$; positive NAO years: $Z = 1.11$, $P = 0.17$).

4.4 Discussion

Overall, there was little evidence that hybrid flickers had either reduced or greater survival relative to parental forms; survival was independent of phenotype. Instead,

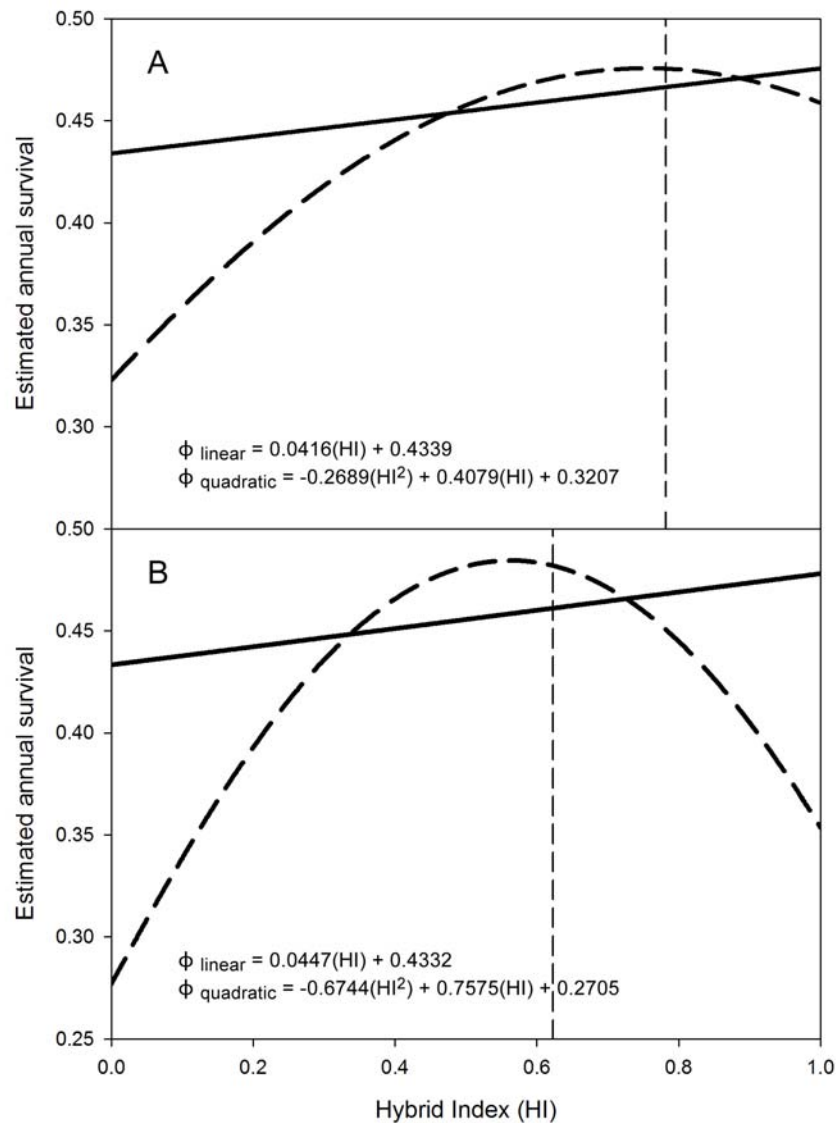


Figure 4.2 Estimated annual survival of northern flickers at Riske Creek, British Columbia based on linear (solid line) and quadratic (dashed line) relationships of HI1 (A) and HI3 (B). HI1 is the sum of 5 plumage traits while HI3 is the score of the tail feather using a spectrophotometer. Hybrid Index (HI) ranges from 0 (pure yellow-shafted flicker) to 1 (pure red-shafted flicker). The vertical dashed line is the population mean for each HI.

the factor that seemed to have the greatest influence on annual survival was weather; strong positive phases of NAO, which result in above average temperatures in the east, were associated with low flicker survival while the negative phases with their below-average temperatures and increased snow cover in the east were associated with high apparent survival. If the different phenotypes of flickers from Riske Creek overwinter in different areas, one would predict that weather might affect the phenotypes differently, but only one model supported an interaction effect between NAO and HI in the models (Table 4.1). However, consistent with Fisher and Wiebe (2006a), sex differences in survival were weakly supported in one model.

Large-scale climatic variations, such as NAO and ENSO (El Niño/Southern Oscillation), are known to influence survival of birds during the wintering periods through increased or decreased precipitation (Sillett et al. 2000; Mazerolle et al. 2005a). North American effects of NAO are considered centered over the eastern United States and Canada (Wallace and Gutzler 1981) and would seem to have little relevance for flicker survival in western North America. However, more recently the NAO has been shown to influence weather throughout North America (Thompson and Wallace 2001) and Nott et al. (2002) found relationships between winter NAO and reproductive success for temperate migrants breeding in the Pacific Northwest. It is possible that the NAO, which is generally an eastern-based weather pattern, could influence western areas where flickers overwinter and therefore correlate with several activities in the annual cycle such as breeding or migration (chapter 2). If so, dynamics of so-called stable hybrid zones could be controlled by annually variable continental weather patterns that must be considered when describing ecological selection gradients that have been considered static on the landscape.

Support for models with constant survival regardless of sex or phenotype is consistent with Fisher and Wiebe (2006a). This was particularly evident in the HI3 analysis using the score from the spectrophotometer of the tail feather where the four models with constant survival were among the top models (Table 4.1). In the case of HI3, stronger support for reduced parameter models in comparison to HI1 is probably a result of smaller sample sizes for HI3 caused by not sampling tail feathers during some intervening years. Despite HI3 being normally distributed and truly continuous, HI1 likely represents a more reliable estimator of parameter values because it is based on multiple traits rather than simply tail colour to designate an individual's hybrid status and has a larger sample associated with continuous mark-resighting over all years.

Mark-recapture analyses are unable to differentiate between death and permanent emigration from a study area (Baker et al. 1995). When breeding dispersal is high, survival will be underestimated but even more so when detection probability (resighting rate) is low (Cilimburg et al. 2002). Resighting rate in this study was >80% which is higher than the 20-60% rate commonly reported in other studies of passerines (Conway et al. 1995; Bayne and Hobson 2002). Although one model of HI3 suggested resighting efficiency was lower for hybrid flickers than pure phenotypes, this was not the case for HI1, and so it is unlikely to be a strong biological effect. In any case, MARK adjusts for resighting efficiency when calculating survival estimates. When plotted according to model parameters, hybrid survival was higher than pure phenotypes (Fig. 4.2), but the conclusion from model selection is that flicker survival is not significantly related to phenotype.

Survival of hybrids under natural conditions is understudied because the best estimates require long-term data, large sample sizes, and great effort to resample

(resight) individuals. Nevertheless, one needs to measure both survival and fecundity to estimate fitness because the parameters sometimes show conflicting patterns. For example, Rowher (2004) used age ratios to determine that survival of pure Townsend's warblers (*Dendroica townsendi*) and hybrids was lower than pure hermit warblers (*D. occidentalis*). Despite this, the range of hermit warblers is retracting because Townsend's are dominant (Pearson and Rohwer 1998, 2000). Given that annual reproductive success does not differ among flicker phenotypes (see chapter 3) and survival also does not seem to vary significantly, the overall fitness of hybrid flickers on my study area seems to be equivalent to parental types.

Recruitment is difficult to measure in open populations when juveniles disperse great distances. I did not model survival of fledglings because it is clear that the 3.6% return rate of nestlings to the local population is mainly a result of high dispersal. Since no banded fledglings were subsequently recovered breeding outside my study area, it is impossible to test whether natal dispersal distances differ among phenotypes. Assuming it does not, the fact that the phenotypes of local recruits were the same as the phenotypes of the fledging cohort the previous year suggests no differences in survival of fledglings according to phenotype. In other words, there is no evidence that post-fledging mortality differs according to hybrid status and, in particular, hybrids do not suffer increased mortality through obvious endogenous selection.

Understanding natal dispersal, settlement and survival tendencies is required to fully understand stability of the zone and how selection operates within it. Where there is selection against hybrids, individuals dispersing in a hybrid zone limit the width of the zone (Barton and Gale 1993) but also the rate of movement that a zone can move via introgression. In many other studies of hybrid zones such as in mammals (*Thomomys*;

Hafner et al. 1983), anurans (*Bombina*; Szymura and Barton 1986), and plants (*Pinus*; Millar 1983) dispersal distances per generation do not exceed the width of the zone.

Hybrid zones explained by hybrid superiority should be located in vegetation transition areas (i.e. ecotone habitats) where exogenous selection should favour hybrid individuals (Moore 1977; Barton and Hewitt 1985). If so, dispersal should be independent of zone width because the zone is dictated by these ecological parameters and thus individuals that disperse outside the habitats that they are best adapted should be selected against (Barton and Hewitt 1985). Although the width of the flicker hybrid zone is somewhat greater than 300 km in most places (Moore 1995), it is certainly less than this in areas of Nebraska and Alberta (see Figure 2.2 in chapter 2). Average natal dispersal distances of flickers have been estimated at 100 km, but this is based on only three individuals (Moore and Buchanan 1985). With such a large proportion of offspring dispersing long distances it should not be unusual for pure yellow or especially red yearling immigrants to settle and recruit locally into my population.

In sum, hybrid phenotype is related neither to the annual reproductive success nor survival of individuals in the northern part of the hybrid zone in central British Columbia. Therefore, there is no strong evidence that the BSHS operates in the north, as it may in the south. Exogenous selection on phenotypes related to environmental gradients may not be as evident in intermountain habitats of British Columbia where environments can vary across short distances compared to the Great Plains in the United States. On a larger geographic scale (e.g. warm and wet coastal B.C. west of the coast range versus the drier east slope of the Rocky Mountains), there may still be exogenous selection that limits long-distance natal dispersal of hybrids and ultimately prevents complete introgression. However, the northern hybrid zone, comprised of migratory

individuals, may be largely a "shadow" of stronger fitness differences in southern portion of the zone. In the future, survival analyses should be conducted on resident flickers on the Great Plains to see whether stronger selection gradients in southern zone could be responsible for the persistence of the hybrid zone.

CHAPTER 5

SUMMARY AND FUTURE DIRECTIONS

5.1 The Nature of Selection in the Northern Flicker Hybrid Zone

Flickers breeding in the northern portion of the hybrid zone showed patterns of assortative mating both in this study (chapter 2) and in a previous study (Wiebe 2000). However, despite the large sample size in this study, positive assortative mating associations were not very strong and suggest that assortative mating may arise passively. Pure red-shafted and yellow-shafted flickers winter on different sides of the Rocky Mountains and thus if they migrate to a common breeding area (i.e. the hybrid zone) they could have different arrival times because the two populations travel different routes. This mechanism could lead to passive assortative mating. Nevertheless, I could not find differences in arrival dates between red and yellow flickers at Riske Creek in one spring. Perhaps timing of arrival does differ in some years, but probably never to the extent documented in some other bird species (e.g. Bensch et al. 1999). However, the average phenotype at Riske Creek correlated with the North Atlantic Oscillation (NAO), an annual variable weather phenomenon and there was a trend for assortative mating patterns to correlate with NAO suggesting that weather influences phenotypes arriving at the northern portion of the flicker hybrid zone at Riske Creek. Annual variation in migratory patterns may therefore influence availability of phenotypes and pairing. The exact wintering areas and migration routes of hybrid flickers are still unknown, however,

so the precise link between weather patterns and continental movements needs further study.

This is the second study to find no fitness advantage to hybrid flickers breeding in the hybrid zone (Moore and Koenig 1986; chapter 3). I found no support that a certain phenotype was reproductively superior to other colour forms. There were no statistical differences in agonistic contests between phenotypes or in their ability to retain breeding territories. Aggressive behaviours were similar between red and yellow flickers during experimental presentations of a taxidermic model although yellow flickers did approach the red model more closely than the yellow model.

Reproductive performance was also similar among the colour forms. Nest initiation date, clutch size, hatching success, and number of fledglings did not differ among yellow, orange and red males and females and between phenotypically similar and dissimilar pairs. Similar nest success among colour groups further suggested that no one colour was more likely to have their nest depredated. Other studies have looked at return rates (Trombino 1998) or estimated survival of broad classified groups (Rohwer 2004) to determine mortality rates of hybrids, but none has model survival based on a hybrid index. I found survival was best modeled as constant with respect to sex but with annual variation associated with weather (NAO). There was no support that hybrids had either significantly higher or lower survival than purer phenotypes.

With equivalent reproduction and survival among phenotypes, the prediction of reduced hybrid fitness (dynamic-equilibrium hypothesis) was not supported. However, I also failed to find increased hybrid fitness to support the BHSH because hybrid phenotypes did not perform better than purer red and yellow individuals. Thus, there

seems to be no barrier to introgression on my study site in the hybrid zone and the hybrid zone should widen and eventually disappear.

There are a couple of reasons why the hybrid zone may persist in the north. Annual changes in selection pressure could prevent introgression of hybrid genes throughout the zone if selection favours red-shafted genes in some years and yellow-shafted genes in other years so that neither form comes to dominate (e.g. Grant and Grant 1993). If selection varies evenly between the two forms it is possible that the zone could be maintained over the long-term and appear stable (Grant and Grant 1992). Secondly, environmental gradients may keep the populations separate in the southern part of the zone even though such gradients are not as distinct and effective in the north.

5.2 Future Directions

My research suggests there may be different dynamics (mating patterns and reproductive success) operating in hybrid flickers in the northern (migratory) and southern (resident) populations. More detailed studies on pairing, reproduction and survival are needed in the southern portion of the hybrid zone to rigorously test whether the BSHS does operate there.

Although my results pointed to a link between continental weather patterns, availability of phenotypes in spring, and assortative pairing, one of the greatest shortcomings was the inability to pinpoint if individuals of different colours segregate on wintering grounds or travel along different migration routes despite the large ramifications this may have on the dynamics of the zone. Several aspects of this shortcoming could be addressed by conducting sampling along transects through the hybrid zone. For example, I tested the utility of stable isotopes using feathers but could not delineate geographic differences between phenotypes (appendix A) that may be due

to the limitations of elucidating east-west gradients required for flickers (Hobson 2005a) or because all individuals from Riske Creek migrate to the same overwintering location. Approaching this question using stable-carbon and stable-nitrogen isotopes may help to differentiate these populations based on mesic versus xeric environments (appendix A). A more precise, albeit more expensive, approach to determining wintering areas for populations would be to use satellite transmitters affixed to migratory individuals. Placing transmitters on individuals from a transect across the hybrid zone would not only determine exact locations of overwintering individuals and how it changes as one progresses through the zone but would provide details of whether the mechanisms of migration are related to hybrid genotypes or to geographic location (e.g. east or west of the Rockies). Additionally, the influence of weather could be further investigated to determine if local to continental weather patterns influence migration speed, direction, and settling patterns. Satellite transmitters that would provide enough battery power to last one year are currently not available for the small body size of flickers, but may be available in the future.

Differences between migratory and resident populations are made all the more interesting because the northern hybrid zone may be shifting in Alberta (McGillivray and Biermann 1987) which does not seem to be occurring in the south (Moore and Buchanan 1985). The phenotypes at Riske Creek seem to vary on an annual basis (chapter 2) but it is unknown if this is a local phenomenon or can be extrapolated to many populations in the northern hybrid zone. Regular surveys (e.g. Breeding Bird Surveys) of flickers in British Columbia and Alaska that record subspecies or phenotypes may help to determine if there are longer-term directional shifts in

phenotypes (i.e. zone movement) in the north. Regardless, the hybrid zone in the north may be more prone to slight annual shifts due to environmental variability.

The exogenous environmental factors that supposedly maintain the phenotypic clines in the hybrid zone are still poorly known. Moore and Price (1993) offered some insight suggesting that precipitation and evapotranspiration rates show similar clines throughout the southern portions of the hybrid zone. Interestingly, these clines are also correlated with contact zones for several hybridizing species in the Great Plains (Rising 1983), commonly referred to as a suture zone (Remington 1968; Swenson and Howard 2004; Swenson 2006). This suggests that some similar exogenous factor(s) such as wet and dry-adapted phenotypes is responsible for the many contact zones that occur in the Great Plains (Moore and Price 1993).

Two approaches are possible to better understand the exogenous controls of these zones. The first is to correlate environmental factors with reproductive success. A more rigorous approach might be to translocate the different phenotypes in a transect across the zone as has been done with hybrid chickadees in the eastern United States (Bronson et al. 2003a). However, such an experiment is difficult for migratory species such as flickers, and the sample sizes needed to detect reproductive or survival differences would make such a study logistically difficult.

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APPENDIX A

STABLE HYDROGEN ISOTOPES DO NOT DELINEATE DIFFERENT WINTERING DISTRIBUTIONS OF MIGRATORY NORTHERN FLICKERS BREEDING IN THE HYBRID ZONE

Introduction

Linking breeding and wintering locations for migratory birds has been at the center of recent research (Hobson et al. 2004; Rubenstein and Hobson 2004) because carry over effects from a wintering location can influence breeding and thus fitness (Norris et al. 2004; Studds and Marra 2004; Norris 2005; Norris and Taylor 2006). Biologists therefore need tools to connect locations where organisms have been during different stages of their annual cycle. Because of the low encounter rates using traditional mark-recovery analyses (Hobson 2003), recent approaches have incorporated genetics markers (Clegg et al. 2003; Boulet et al. 2006) and stable isotopes (Mazerolle et al. 2005b; Norris et al. 2006) to delineate populations. Stable isotope measurements have been used to determine allopatric winter distributions for morphologically similar populations (Bensch et al. 1999) that migrate to a common breeding area known as a migratory divide (Chamberlain et al. 2000; Mehl et al. 2004; Bearhop et al. 2005). If interbreeding populations overwinter in allopatry, different selection pressures could influence behaviours such that migration timing and arrival times could differ between populations and could influence mate choice.

Northern populations of northern flickers (*Colaptes auratus*) are generally migratory and wintering distributions are well delineated for the parental forms; yellow-shafted flickers winter to the east of the Rocky Mountains while red-shafted flickers winter to the west (Figure A1; chapter 2). Migration and wintering locations of flickers that breed in the hybrid zone are less well determined and because sightings of colour forms outside of their expected winter distributions are uncommon, it is generally assumed that the migration direction and overwintering location is based on the genetics of the individual (e.g. Berthold et al. 1992). Therefore, in the middle of the hybrid zone we might expect there should be a split between the directions individuals migrate. For example, many eastern and western forms of birds meet in the Great Plains of North America and form hybrid zones (Moore and Price 1993), however, sightings of individuals away from their expected winter range is uncommon and thus there is little evidence that migration routes and winter location is determined randomly. If flickers from the hybrid zone winter in allopatry, it is possible that migration schedules in spring could result in staggered arrival patterns leading to passive assortative mating (chapter 2). Because yellow flickers are rare in the hybrid zone at Riske Creek and therefore it is difficult to obtain many band recoveries, I wanted to determine the wintering location of

these individuals compared to the more abundant red-shafted flickers using stable isotope analysis.

Methods

Birds that show a complete pre-basic moult often begin with flight feathers, continue with body feathers and finish in the neck and head region (Pyle 1997). Besides flight feathers, the moult regime of flickers is poorly known (Test 1945) and they do not have a prealternate moult on the wintering grounds (Pyle 1997). However, migratory woodpeckers can have a protracted pre-basic moult with feather replacement continuing from winter to the following summer (Pyle 1997). Test (1945) claimed that flight feather moult can continue until September and so I assumed head feathers are replaced sometime after this date. Therefore, head feathers of adult flickers should provide an isotopic signature representative of the post-breeding period during late autumn migration or of a wintering location.

I collected head feathers from 10 yellowish and 10 reddish flickers breeding at Riske Creek, British Columbia as well as from 10 nestlings born locally in 2005. I collected feathers from nestlings born at Riske Creek for two purposes: first, to acquire a local deuterium content of the feather (δD_f), and second, to compare to adult feathers to determine if indeed adults moulted feathers off-site. I collected five head feathers from each adult flicker and two back feathers from each nestling.

Feathers were stored in paper envelopes between collection and lab preparation. Feathers were rinsed in 2:1 chloroform: methanol solution and allowed to air dry. I measured 0.33 - 0.37mg of feather into silver capsules and combusted using continuous-flow isotope ratio mass spectrometry (Wassenaar and Hobson 2003). Deuterium values are reported in units per mil (‰) in delta notation and normalized on the VSMOW-SLAP scale. Although I did not determine repeatability of feather values, other studies have found high repeatability of δD_f of head feathers, suggesting strong estimates of growing location of feathers (Mazerolle et al. 2005b).

Results

Isotopic feather signatures were significantly different between those grown by nestlings at Riske Creek and adults that moulted the previous fall ($t = 4.33$, $df = 28$, $P < 0.001$; Table A1). However, there were no difference in the isotopic signatures between the adult red and yellow flickers ($t = 0.56$, $df = 18$, $P = 0.58$; Table A1).

Discussion

The head feathers that I sampled did differ isotopically from locally grown feathers, and had a more "southern" isotope signature but I could not determine if the feathers were grown on the wintering grounds or during migration. It is unlikely that all adults were in the same location when moulting because winter recoveries of flickers from Riske Creek vary between southern Canada to California (chapter 2).

There was no difference in feather signatures between yellowish and reddish flickers. Hydrogen isotope contours of western Canada are such that even in the early stages of migration, all flickers departing Riske Creek could have occurred within the same general latitude regardless of whether they were heading southeast or southwest (Figure A1; Meehan et al. 2004). However, even if a difference between red and yellow adults had been found, it would not necessarily prove that the phenotypes winter in allopatry.

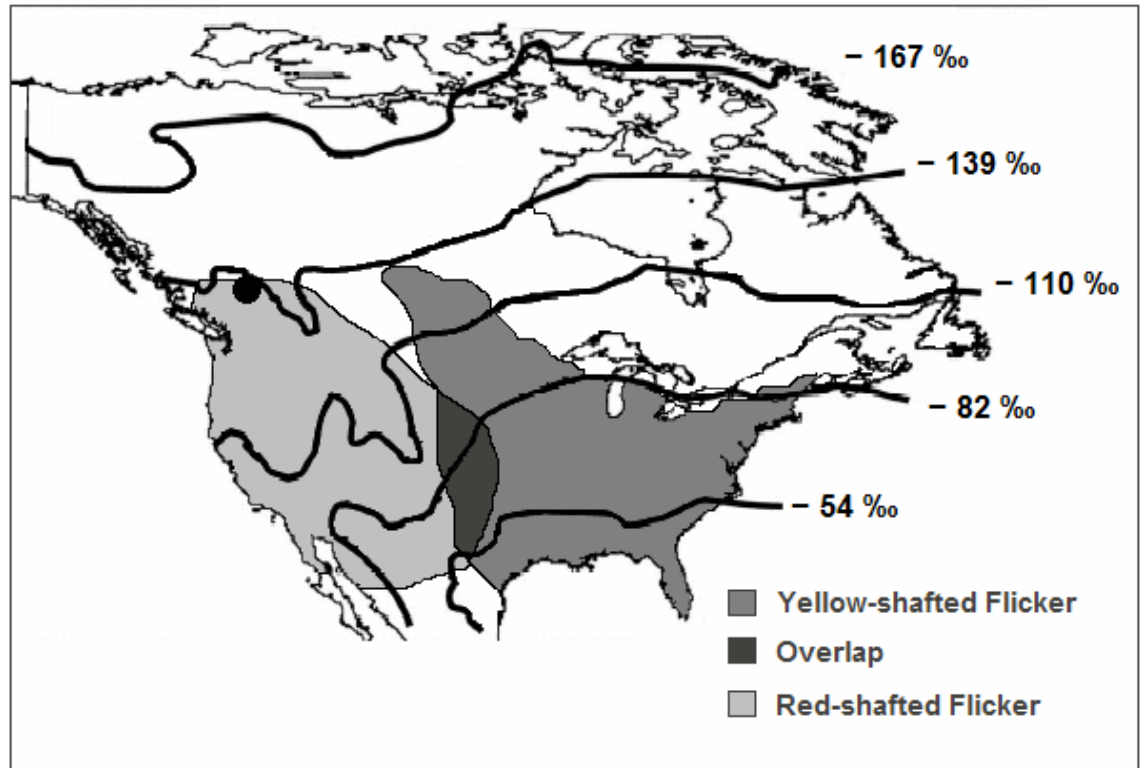


Figure A1. The approximate wintering range of yellow-shafted and red-shafted flickers according to Christmas Bird Count data (National Audubon Society 2002) and North American deuterium values of feathers adapted from Meehan et al. (2004). Feather values incorporate an isotopic discrimination factor of -25‰ between δD of precipitation and δD of feathers (δD_f) (Wassenaar & Hobson 2001). The location of Riske Creek is marked by a circle.

Table A1 Mean, standard error and sample size of feather deuterium values in t-test comparisons between nestling and adult flickers and between yellow and red adults from Riske Creek, British Columbia.

Group	δD_f (‰)	SE	n	P
Nestlings	-137.7	0.8	10	P < 0.001
Adults	-120.3	2.8	20	
Yellow	-118.7	5.0	10	P = 0.58
Red	-121.9	2.7	10	

Individuals may also adopt different signatures if they differ in the location and speed of migration. Without an idea of the variation in body and head feather moult of flickers it is difficult to determine when exactly head feathers are moulted and if all individuals whose feathers were sampled moulted at the same stage of migration or wintering. This shortcoming severely restricts the ability to determine if reddish and yellowish flickers from Riske Creek winter in allopatry. Nevertheless, my results show that red and yellow flickers moulted their head feathers in the same isocline reading as one another within approximately 1.5° of latitude (~150 km) (Meehan et al. 2001).

Differentiating the wintering areas of red and yellow flickers may be difficult because of the limitation of deuterium stable isotopes to show east-west gradients (Hobson 1999, 2005b). A further approach may be to use ¹³C (carbon) and ¹⁵N (nitrogen) stable isotopes that can differ between moist, mesic environments and dry, xeric environments (Marra et al. 1998; Rubenstein et al. 2002) and are promising because the flicker hybrid zone shows phenotypic clines where red-shafted flickers occupy the hotter, drier west and yellow-shafted phenotypes occupy the moister and wetter east in the southern United States (Moore and Price 1993). These techniques have been used in willow warblers (*Phylloscopus trochilus trochilus* and *P. t. acredula*) to differentiate allopatric wintering ranges of individuals that breed across a migratory divide in Scandinavia (Chamberlain et al. 2000). In North America, classification tree analysis using deuterium, carbon, nitrogen and sulphur has been used to differentiate natal areas between Alaska and the mid-continent prairies of northern pintail (*Anas acuta*; Hebert and Wassenaar 2005). Additionally, hydrogen, carbon and nitrogen isotopes have been used to trace flight feather moult locations after the breeding season in king eiders (*Somateria spectabilis*; Knoche et al. 2007) and delineate the unknown winter range of coastal-dependent swamp sparrows (*Melospiza georgiana nigrescens*; Greenberg et al., in press).